



## Research article

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# Evolution of genital asymmetry, exaggerated eye stalks, and extreme palpal elongation in *Panjange* spiders (Araneae: Pholcidae)

Bernhard A. HUBER<sup>1,\*</sup> & Olga M. NUÑEZA<sup>2</sup>

<sup>1</sup>Alexander Koenig Research Museum of Zoology, Adenauerallee 160, 53113 Bonn, Germany.

<sup>2</sup>Department of Biological Sciences, Mindanao State University - Iligan Institute of Technology, Tibanga, Iligan City 9200, Philippines.

\* Corresponding author: [b.huber@zfmk.de](mailto:b.huber@zfmk.de)

<sup>2</sup> Email: [olgamnuneza@yahoo.com](mailto:olgamnuneza@yahoo.com)

<sup>1</sup>[urn.lsid:zoobank.org:author:33607F65-19BF-4DC9-94FD-4BB88CED455F](http://urn.lsid:zoobank.org:author:33607F65-19BF-4DC9-94FD-4BB88CED455F)

<sup>2</sup>[urn.lsid:zoobank.org:author:6D14FCCC-F148-4293-9F23-0EB5A4119305](http://urn.lsid:zoobank.org:author:6D14FCCC-F148-4293-9F23-0EB5A4119305)

**Abstract.** We describe several new species of the previously monotypic *Panjange lanthana* species group from the Philippines and document their extraordinary morphology. Some species show strong male genital asymmetry, a phenomenon that seems to be exceedingly rare in spiders. Males of most species have eye stalks, and in two species these eye stalks are among the longest ever recorded in spiders. Some species show a tendency for male genital (pedipalp) elongation, and one species has the longest and thinnest palps ever recorded in Pholcidae. A cladistic analysis is performed including all described and several undescribed species of *Panjange* (except for one “problem species”), supporting the *lanthana* group and its close relationship with members of the possibly paraphyletic *cavicola* group. The following eight new species are described: *Panjange malagos* Huber sp. nov.; *Pa. casaroro* Huber sp. nov.; *Pa. camiguin* Huber sp. nov.; *Pa. hamiguitan* Huber sp. nov.; *Pa. isarog* Huber sp. nov.; *Pa. dinagat* Huber sp. nov.; *Pa. marilog* Huber sp. nov.; *Pa. bukidnon* Huber sp. nov.

**Key words.** Genital asymmetry, eye stalks, palpal elongation, sexual selection, *Panjange*, Philippines.

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## Introduction

*Panjange* Deeleman-Reinhold & Deeleman, 1983 spiders are leaf-dwelling pholcids widely distributed in insular Southeast Asia, from Borneo and the Philippines to northern Australia (Huber 2011). They exhibit some of the most extraordinary morphology among Pholcidae. Males of most species have eye stalks, sometimes with long pointed processes; males of some species have unusually elongated pedipalps, which in spiders function as copulatory organs; and females of some species have external portions of their genitalia strongly folded and extensible (Huber 2011). The biological significances of these sexual modifications remain unclear.

The genus has long been divided into three species groups: the *nigrifrons* group on Borneo, the *cavicola* group ranging from Sulawesi to northern Australia, and the *lanthana* group in the Philippines (Deeleman-Reinhold & Platnick 1986; Huber 2011). However, the latter “group” so far consisted of only one species, the very unique type species *Panjange lanthana* Deeleman-Reinhold & Deeleman, 1983, known only from the type series from Luzon. No further *Panjange* species has been known from the Philippines. Here we describe several new species that appear closely related to *Pa. lanthana*, and that show some very unique morphological features, not only among Pholcidae but among spiders in general: genital asymmetry, exaggerated eye stalks, and extreme palpal elongation.

Genital asymmetry is very common in some arthropod groups (such as insects) but very rare in others (such as spiders) (reviewed in Huber *et al.* 2007). Ultimately, the reason for this may be the fact that insects have an unpaired median intromittent organ (the aedeagus) while spider males copulate with a pair of pedipalps (Huber 2010). However, while there are plausible evolutionary routes to asymmetry in insects (related to changes in mating position that in turn are driven by sexual selection; Huber 2010), the origin of spider genital asymmetry is still poorly understood. Two of the new species described below are among the most asymmetric spiders known so far.

Eye stalks are also widespread in arthropods such as crustaceans (e.g., Barnes 1968; Bowman 1984; Zeil *et al.* 1986) and insects (in particular flies: e.g., Burkhardt & de la Motte 1988; Wilkinson & Dodson 1997; Baker & Wilkinson 2001), but very rare in arachnids. Fairly well studied exceptions are certain linyphiid species where the male “head” or ocular area is modified, presumably as a result of sexual selection: males take advantage of the fact that the female mouthparts contact their ocular region during copulation and modify this region in an attempt to manipulate females (e.g., Schaible *et al.* 1986; Vanacker *et al.* 2003; Kunz *et al.* 2012). Usually, these modifications come in the form of low humps or turrets, but rarely also as (unpaired median) stalks, such as in *Walckenaeria acuminata* Blackwall, 1833. In Pholcidae, a similar mating position may explain the repeated origin of male “head” modifications, such as in the genera *Modisimus* Simon, 1893, *Smeringopina* Kraus, 1957, *Pholcus* Walckenaer, 1805, *Leptopholcus* Simon, 1893, and *Panjange* (see e.g., Huber 1997a, 2011, 2013). Two of the new species described below have the longest eye stalks known in Pholcidae, and possibly in spiders.

Elongated male copulatory organs (pedipalps) occur in various spider groups, but the palps are rarely longer than the body (exceptions occur for example in Filistatidae; Marusik & Zamani 2015). The significance of this elongation is poorly understood, and the plausible idea that long palps may save the male from cannibalism has to our knowledge never been tested. In Pholcidae, palpal strength seems to play an important role, often leading to very thick palpal segments (Huber & Eberhard 1997). As a result, elongated (and thus necessarily thin) palps are rare in pholcids, and apparently limited to Southeast Asian leaf dwelling species. The only cases known to us occur in the genera *Calapnita* Simon, 1892 (most notably *C. semengoh* Huber, 2011), in most species of the *Panjange cavicola* group (Huber 2011) and in certain species currently placed in *Pholcus* but possibly close to *Panjange* (such as *Pholcus bohorok* Huber, 2011). In all of them, females have extensible external genitalia (or scapes), suggesting a functional correlation between palp length and scape length. A new species described below has by far the longest and thinnest male palps known in Pholcidae, as well as the longest female scape.

## **Material and methods**

Most of the material studied herein was collected during a recent expedition to the Philippines (Feb.–Mar. 2014). Further specimens came from student projects at Mindanao State University - Iligan Institute of Technology dealing with ecological aspects of pholcid diversity in the Philippines. The material is currently deposited at Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK) and Mindanao State University - Iligan Institute of Technology (MSU-IIT).

Species descriptions are arranged as in the cladogram in Fig. 1. Methods and terminology are as in recent revisions (Huber 2011, 2013). Measurements are in mm unless otherwise noted. Eye measurements are +/- 5 µm. Epigyna were cleared in warm NaOH solution and stained with chlorazol black. For SEM photographs, specimens were dried in HMDS (Brown 1993), and photographed with a Hitachi S-2460 scanning electron microscope. SEM data are presented within the descriptions but are not based on the holotype specimens described. The distribution map was generated with ArcMap 10.0.

The numerical cladistic analyses were done using NONA, version 2 (Goloboff 1993), Pee-Wee, version 2.8 (Goloboff 1997) and TNT, version 1.1 (Goloboff *et al.* 2004, 2008). The matrix is shown in Appendix 1; terminal taxa and characters scored are given in Appendices 2 and 3. All 26 characters are binary. The final matrix can be downloaded at <http://www.pholcidae.de/matrices.html> [accessed 21 Nov. 2015]. Cladogram analysis was done with Winclada, version 1.00.08 (Nixon 2002). See “Cladistic analysis” section below for details of the analyses.

### Abbreviations

The following abbreviations are used in the text:

ALE = anterior lateral eyes

ALS = anterior lateral spinnerets

AME = anterior median eyes

a.s.l. = above sea level

L/d = length/diameter

PME = posterior median eyes

PMS = posterior median spinnerets

In order to avoid confusion, *Panjange* is abbreviated as “*Pa.*”; *Pholcus* is never abbreviated. Further abbreviations used only in figures are explained directly in the figure legends.

### Results

Class Arachnida Cuvier, 1812  
Order Araneae Clerck, 1757  
Family Pholcidae C.L. Koch, 1851

Genus *Panjange* Deeleman-Reinhold & Deeleman, 1983

*Panjange* Deeleman-Reinhold & Deeleman, 1983: 123–124. Type species by original designation: *Panjange lanthana* Deeleman-Reinhold & Deeleman, 1983.

*Panjange* – Deeleman-Reinhold 1986a: 47, fig. 6; 1986b: 220. — Huber 2001: 118–119; 2011: 108–110.

### Note on species groups

Previous work on *Panjange* has identified three species groups, the *nigrifrons* group on Borneo, the widespread *cavicola* group (Sulawesi to northern Australia) and the previously monotypic *lanthana* group on the Philippines (Deeleman-Reinhold & Platnick 1986; Huber 2011). The present cladistic analysis largely recovers these three groups, but the *cavicola* group is considered paraphyletic (Fig. 1).

The present paper focuses on the *lanthana* group. A separate paper on the *nigrifrons* group is in preparation, as is a molecular phylogeny of the entire genus and of its relationships to other Pholcinae.

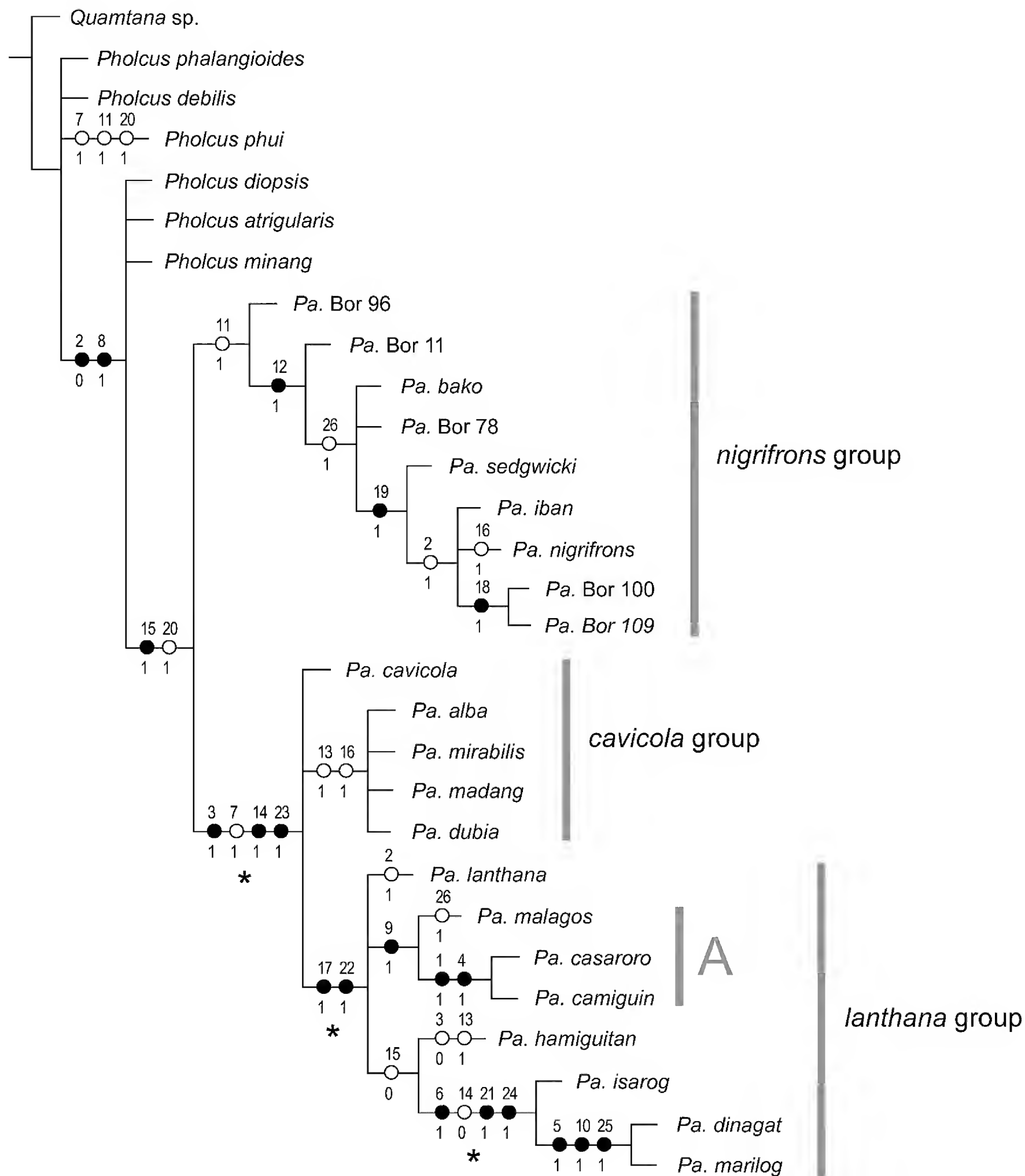
### Identification key

This key is primarily designed to identify species groups of *Panjange* and species of the *lanthana* group. It mostly works for males and females, but females remain difficult to identify. An examination of the

cleared internal genitalia may be necessary (step 7); geography rather than morphology may help to separate females (step 2); in one species, the female is unknown (*Pa. bukidnon* Huber sp. nov.; step 4).

1. Male chelicerae with distal frontal apophyses (fig. 472 in Huber 2011); female epigynal scape short or absent (figs 473, 492 in Huber 2011); known only from Borneo..... *nigrifrons* group
  - Male chelicerae without distal frontal apophyses, only with pair of proximal processes (e.g., Figs 17, 40, 66); epigynal scape long and strongly folded (e.g., Figs 22, 36, 67)..... 2
2. Embolus parallel to male bulbal process (appendix); known from Sulawesi to Australia ..... *cavicola* group
  - Embolus and bulbal appendix pointing in opposite directions (e.g., Figs 18, 64, 69); known from the Philippines only ..... *lanthana* group...3
3. Eight eyes (AME present; lenses clearly visible in dissecting microscope); without pointed processes arising from male eye triads (fig. 441 in Huber 2011); procurus with two distal hinged processes (figs 436, 437 in Huber 2011).....*Pa. lanthana* Deeleman-Reinhold & Deeleman, 1983
  - Six eyes (AME absent; rarely tiny, barely visible in dissecting microscope and apparently non-functional: Fig. 45), with pointed processes arising from male eye triads (e.g., Figs 17, 28, 66, 76); procurus with only one distal hinged process ..... 4
4. Procurus extremely wide and strongly curved (Fig. 91); eye stalks short, with spines contacting each other (Fig. 90); bulbal processes (embolus and appendix) very short (Fig. 91)..... *Pa. bukidnon* Huber sp. nov.
  - Procurus, male ocular area, and bulbal processes different ..... 5
5. Male palpal segments (distal of trochanter) extremely long (femur about 15 × as long as wide; Figs 64, 65); female epigynal scape extremely long (Fig. 67) .....*Pa. hamiguitan* Huber sp. nov.
  - Male palpal segments shorter (femur less than 7 × as long as wide; e.g., Figs 19, 25, 39); female epigynal scape shorter (e.g., Figs 22, 29, 72) ..... 6
6. Male clypeus without spines; dorsal tarsal elongation very long (Figs 18, 24); male procurus asymmetric; female epigynal scape directed toward posterior..... 7
  - Male clypeus with spines (Figs 71, 76, 81); dorsal tarsal elongation short (Figs 70, 75, 80); male procurus symmetric; female epigynal scape directed toward anterior (Figs 72, 77, 82) ..... 9
7. Male eye stalks short (Fig. 17); spines on male eye stalks short, not contacting each other; pore plates round (Fig. 23)..... *Pa. malagos* Huber sp. nov.
  - Male eye stalks very long (Figs 28, 35); spines on male eye stalks long, contacting each other (Fig. 49); pore plates oval (Figs 30, 37)..... 8
8. Male palpal trochanter with only one long retrolateral apophysis (Fig. 25); male palpal tarsal elongation widening distally (Fig. 24); female epigynal scape with two lobes (Fig. 29)..... *Pa. casaroro* Huber sp. nov.
  - Male palpal trochanter with two short retrolateral apophyses (Fig. 39); male palpal tarsal elongation not widening distally (Fig. 38); female epigynal scape simple (Fig. 36) .....*Pa. camiguin* Huber sp. nov.
9. Appendix of genital bulb with simple curved tip (Fig. 69); male palpal retrolatero-ventral trochanter apophysis with simple rounded tip (Fig. 70); female epigynal scape without widening (Fig. 72) ..... *Pa. isarog* Huber sp. nov.
  - Appendix of genital bulb with bifid tip (Figs 74, 79); male palpal retrolatero-ventral trochanter apophysis bifid (Figs 75, 80); female epigynal scape with widening (Figs 77, 82) ..... 10

10. Retrolateral process on procurus massive, with parallel ridges (Fig. 75); female internal genitalia with large lateral structures and elongate pore plates (Fig. 78) ..... *Pa. dinagat* Huber sp. nov.  
 – Retrolateral process on procurus smaller, with two pointed tips (Fig. 80); female internal genitalia without large lateral structures and roundish pore plates (Fig. 83) ..... *Pa. marilog* Huber sp. nov.



**Fig. 1.** Strict consensus of two most parsimonious cladograms of *Panjange* Deeleman-Reinhold & Deeleman, 1983 resulting from analyses of the matrix in Appendix 1 using equal character weights, successive weighting, and implicit enumeration. Only unambiguous character changes are shown. A = clade with asymmetric male palps; \* = positions of *Pa. bukidnon* Huber sp. nov. in preliminary cladistic analyses. See Cladistic analysis section for further details.

### Cladistic analysis

Preliminary analyses including all available species of *Panjange* (all 18 described species plus five undescribed species) revealed that the highly aberrant *Pa. bukidnon* Huber sp. nov. was also the most difficult to place in the cladogram. It ended up at three different positions, resulting in many trees and a consensus with large polytomies. For this reason, *Pa. bukidnon* Huber sp. nov. was deleted from the final matrix. It may be correctly placed in the *lanthana* group but its sister taxon remains unknown (see Monophyly and relationships below).

One potentially informative character system was also largely deleted from the final matrix. The apophyses and processes on the male palpal trochanter come in a wide variety of numbers, shapes and positions, and it seemed impossible to code them in a convincing way. Only one detail was left in the matrix (Appendix 3, character 10).

Using NONA with hold/100, mult\*200 (or hold/10; mult\*10.000), and amb- for the matrix in Appendix 1 and equal character weights resulted in two most parsimonious cladograms with a length of 37 (Ci = 70; Ri = 90). Variation occurred only among outgroup taxa and in the support for the monophyly of *Panjange* (characters 15 and 20, or only character 20). The cladogram shown in Fig. 1 is the strict consensus of these two cladograms.

Using TNT with the implicit enumeration algorithm resulted in the same two trees, as did successive weighting in NONA (with the consistency index as weighting function). Implied weighting in Pee-Wee (which resolves character conflict in favor of the characters that have less homoplasy) was used with various settings of the constant of concavity K (1–6) to explore the stability of different clades under different weighting regimes. Major differences to the tree shown in Fig. 1 occurred only with K=1 and K=2, which resulted in large polytomies and no support for the monophyly of *Panjange*. However, even in these trees, the monophyly of the *lanthana* group was consistently recovered as was its close relationship to the *cavicola* group. The only difference within the *lanthana* group concerned the position of *Pa. hamiguitan* Huber sp. nov., which was not sister to *Pa. isarog* Huber sp. nov. + (*Pa. dinagat* Huber sp. nov. + *Pa. marilog* Huber sp. nov.) but placed in a basal tetrachotomy.

### *Panjange lanthana* group

#### Diagnosis

Males are easily distinguished from congeners in other species groups of *Panjange* by the unique processes of the genital bulb (embolus and appendix), pointing in opposite directions (Figs 18, 64, 69). Females differ from members of the *nigrifrons* group by their long folded scapes (Figs 22, 67, 72) but are in general similar to females of the *cavicola* group. Other leaf-dwelling pholcids in the Philippines differ from *Panjange* as follows: *Calapnita* with longer abdomen that is monochromous and dorso-posteriorly not angular; male eyes on very low humps; embolus parallel to bulbal appendix. An undescribed group of leaf-dwelling *Pholcus* species differs from Philippine *Panjange* species as follows: dorsal process on procurus; embolus parallel to bulbal appendix; short male eye stalks without pointed processes; and epigynum without long folded scape.

#### Description

##### Male

MEASUREMENTS. Total body length ~4.0–5.5; carapace width 0.9–1.2; leg 1 length ~30–45; tibia 1 length ~8.0–10.5; tibia 2/tibia 4 length 1.10–1.25; tibia 1 L/d ~95–110.

**COLOR.** In life (Figs 2–15) mostly pale ochre-yellow to whitish, ocular area with brown mark, sternum whitish, legs with dark patellae and tibia-metatarsus joints; abdomen with dark brown to black marks dorsally and laterally, sometimes partly reddish.

**BODY.** Carapace without median furrow; ocular area raised, eye triads on stalks of variable length (e.g., Figs 17, 28, 66, 71), often with pair of additional pointed processes arising from near PME (absent only in *Pa. lanthana*). AME usually absent, clearly present only in *Pa. lanthana*, present but tiny and barely visible in *Pa. camiguin* Huber sp. nov. males (Fig. 45). Clypeus high, either unmodified or with ~20–25 short spines (Figs 84, 85), sometimes in addition to stronger hairs below ocular area (Fig. 84). Abdomen cylindrical, angular above spinnerets (Figs 2, 9). Male gonopore with four epiandrous spigots (Figs 60, 88); each ALS with large widened spigot, pointed spigot, and six cylindrically shaped spigots (of varying sizes; Figs 32, 62); PMS with two spigots each (Fig. 63).

**CHELICERAE.** With only one pair of frontal processes proximally, without distal apophyses (Figs 17, 47, 84); without modified hairs; without stridulatory ridges.

**PALPS.** Coxa usually unmodified, in *Pa. hamiguitan* Huber sp. nov. and *Pa. bukidnon* Huber sp. nov. with small ventral apophysis (Figs 65, 92); trochanter and femur very variable, with species-specific sets of humps, short processes, and more complex apophyses; patella short to longer than wide; tibia with two trichobothria; palpal tarsus usually with whitish dorsal elongation carrying tarsal organ (e.g., Figs 19, 25, 65), rarely short (e.g., Figs 70, 75), absent in *Pa. bukidnon* Huber sp. nov. (Fig. 92); palpal tarsal organ capsulate (Fig. 89); procurus usually consisting of proximal and distal part connected by membranous hinge (e.g., Figs 18, 64, 80), but not hinged in right palps of asymmetric species; parallel ridges on procurus sometimes distinct (e.g., Figs 18, 26, 52), sometimes indistinct or absent; bulb with strong proximal sclerite (e.g., Figs 18, 69), with two processes pointing in opposite directions: appendix toward ventral, embolus toward dorsal.

**LEGS.** Without spines, without curved hairs, few vertical hairs; retrolateral trichobothrium very proximal (tibia 1: at 2–4% of tibia length), prolateral trichobothrium absent on tibia 1, present on other tibiae. Tarsus 1 with ~30 pseudosegments, sometimes very indistinct; tarsus 4 with single row of ventral comb-hairs of the *Pholcus*-type (cf. Huber & Fleckenstein 2008) (Fig. 58).

### **Female**

Similar to male but without eye stalks; eye triads on low humps (Fig. 46); clypeus and chelicerae unmodified; legs slightly shorter than in male. Epigynum weakly sclerotized, with more or less long, folded and extensible scape directed either toward posterior or toward anterior (e.g., Figs 22, 36, 72); sometimes widened at about half length (Figs 77, 82). Internal genitalia with pair of pore plates of variable shape.

### **Monophyly and relationships**

The monophyly of the *Pa. lanthana* group is consistently supported by two characters: the small ventral process distally on the proximal part of the procurus (character 17; Figs 25, 70), and the unique direction of the embolus, pointing in an opposite direction than the appendix rather than lying parallel to it (character 22; Figs 18, 64, 69).

The closest relatives of the *lanthana* group are probably members of the *Pa. cavicola* group. This relationship has been suggested before (Huber 2011) and is here supported by numerous characters: hooked rather than straight spines in ocular area (character 3; Figs 48, 87); absence of distal cheliceral apophyses (character 7; Figs 17, 47, 66); strong palpal tarsal elongation (character 14; Figs 19, 39, 65); and long strongly folded epigynal scape (character 23; Figs 22, 36, 72).

Within the *lanthana* group, the monophyly of three species *Pa. malagos* Huber sp. nov. + (*Pa. casaroro* Huber sp. nov. + *Pa. camiguin* Huber sp. nov.) is supported only by the asymmetry of the male procurus (character 9). A second species group, *Pa. isarog* Huber sp. nov. + (*Pa. dinagat* Huber sp. nov. + *Pa. marilog* Huber sp. nov.) is strongly supported: male clypeus with spines (character 6; Figs 84, 85); male palpal tarsal process secondarily short (character 14; Figs 70, 75, 80); uncus-like process arising from proximal bulbal sclerite (character 21; Figs 70, 80); and epigynal scape directed toward anterior (character 24; Figs 72, 77, 82). The sister taxa of *Pa. lanthana* and *Pa. hamiguitan* Huber sp. nov. remain unclear. In Fig. 1, *Pa. hamiguitan* Huber sp. nov. is placed as sister to *Pa. isarog* Huber sp. nov. + (*Pa. dinagat* Huber sp. nov. + *Pa. marilog* Huber sp. nov.), but this is weakly supported by the secondary reduction of ridges on the procurus and was not recovered in all analyses (see above).

Entirely dubious is the position of *Pa. bukidnon* Huber sp. nov. (excluded from the analysis for reasons detailed above; see “Cladistic analysis”). In preliminary analyses including *Pa. bukidnon* Huber sp. nov., it ended up at three different positions, indicated in Fig. 1 by asterisks: (1) as sister to the *lanthana* + *cavicola* groups; (2) as sister to the *lanthana* group; or (3) as sister to *Pa. isarog* Huber sp. nov. + (*Pa. dinagat* Huber sp. nov. + *Pa. marilog* Huber sp. nov.). It shares one of the synapomorphies of the *lanthana* group (embolus pointing in opposite direction than appendix) but not the other (ventral process on procurus). The parallel tips of the ocular spines (Fig. 90) remind of *Pa. casaroro* Huber sp. nov. + *Pa. camiguin* Huber sp. nov. while the small rounded process between appendix and genital bulb (Fig. 91) reminds of *Pa. dinagat* Huber sp. nov. + *Pa. marilog* Huber sp. nov. The procurus is highly autapomorphic. It seems that only the discovery of the unknown female and/or molecular data may solve this issue.

### Natural history

Most species seem to have low abundances and very patchy distributions, with few specimens found within a very small area and none in surrounding areas of apparently similar vegetation. This may have been related to the low abundance and patchiness of suitable large leaves. Specimens were usually collected between about 50 cm above ground to about 2 m, and they are likely to occur also in higher strata of the forest, possibly in higher abundances. The web is a domed sheet, most of which is closely attached to the underside of a leaf. The extremely fine silk is poorly visible except when the sheet is viewed directly from the side. Egg sacs are only slightly elongated and covered by a barely visible layer of silk (Figs 3, 8, 12). In one case (*Pa. camiguin* Huber sp. nov.; Fig. 8), eight of ten eggs in an egg sac were parasitized by a parasitic wasp.

### Composition

As construed here, the *Panjange lanthana* group now contains nine species (including the dubious *Pa. bukidnon* Huber sp. nov.). Judging from known distribution patterns and from the large number of poorly sampled islands, the group may well contain several times as many species.

### Distribution

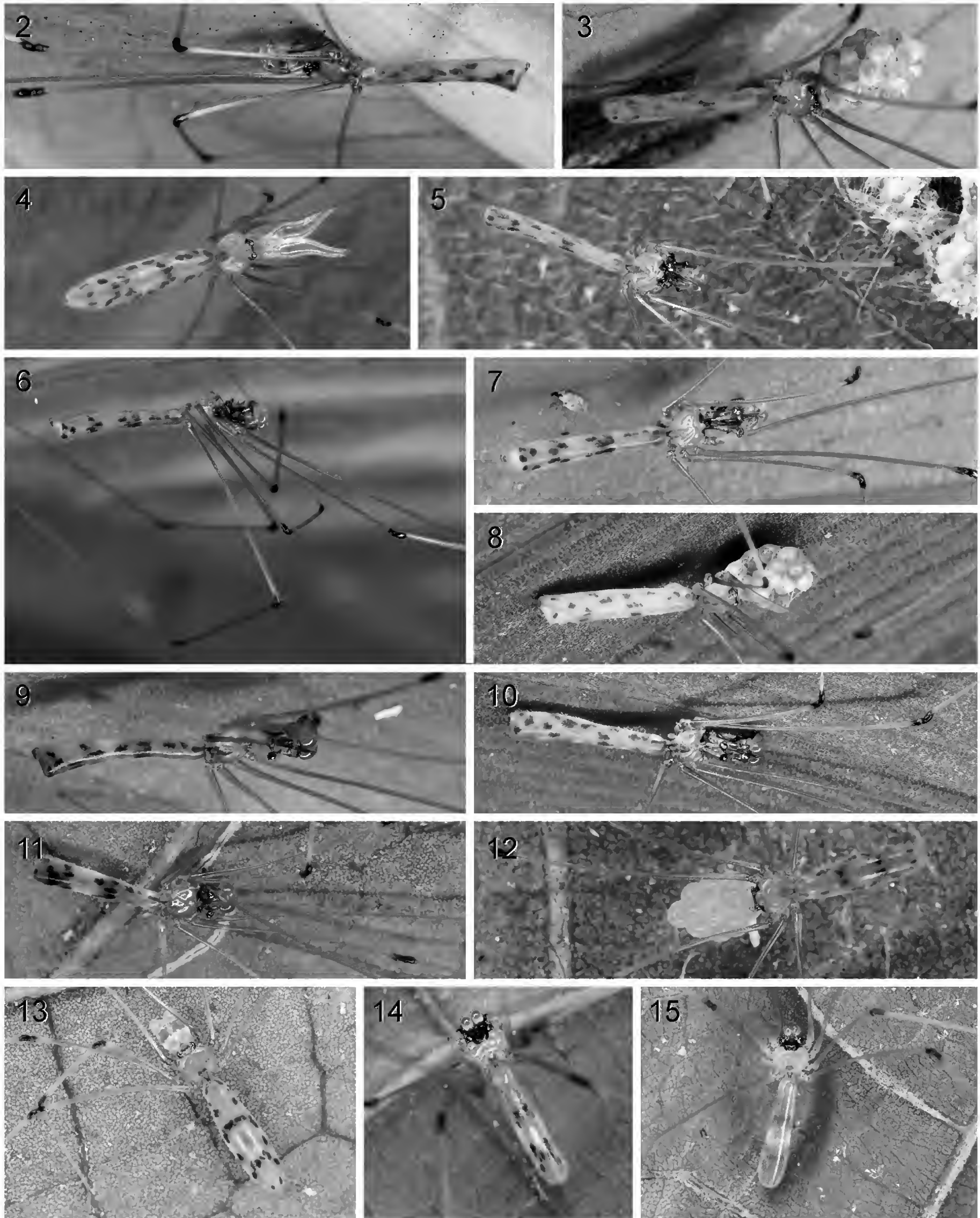
Known from the Philippines only (Fig. 16).

*Panjange lanthana* Deeleman-Reinhold & Deeleman, 1983  
Figs 2–4

*Panjange lanthana* Deeleman-Reinhold & Deeleman, 1983: 124, figs 1–9 (♂♀).

*Panjange lanthana* – Huber 2011: 111–114, figs 436–58, 765–66, 786, 788 (♂♀).

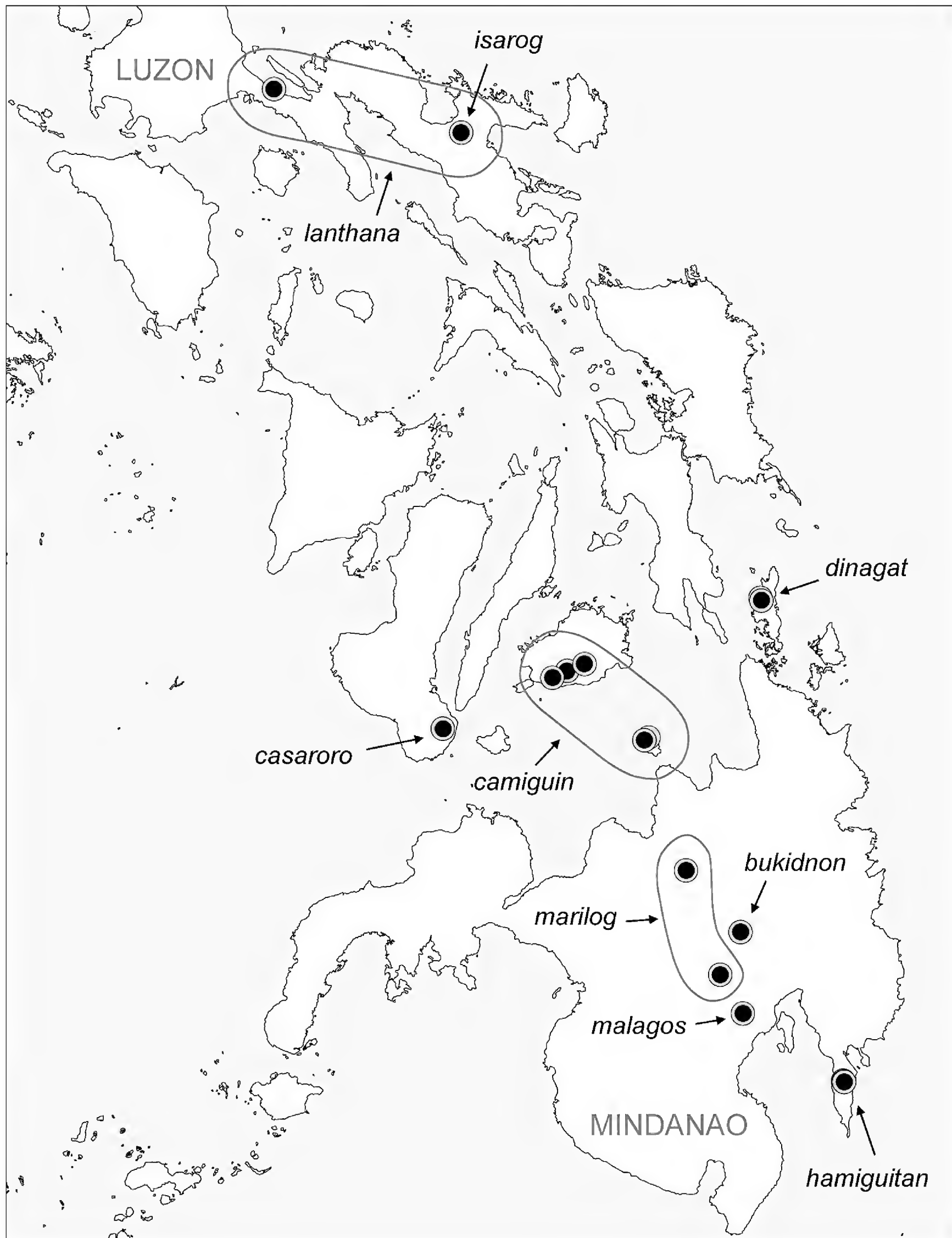




**Figs 2–15.** Live specimens. 2–4. *Pa. lanthana*, Mt. Isarog, ♂, ♀ with eggsac, and penultimate ♂. 5. *Pa. malagos* Huber sp. nov., ♂. 6–7. *Pa. casaroro* Huber sp. nov., ♂♂. 8–10. *Pa. camiguin* Huber sp. nov. 8. ♀ with parasitized eggsac, from Camiguin Island. 9. ♂ from Bohol Island. 10. ♂ from Camiguin Island. 11–13. *Pa. dinagat* Huber sp. nov., ♂, ♀ with eggsac, and penultimate ♂. 14–15. *Pa. marilog* Huber sp. nov., ♂♂ showing color variation.

**Note**

Previously, the type species *Pa. lanthana* was both geographically and systematically isolated. It was the only known Philippine representative of the genus and single representative of the *lanthana* “group” (Deeleman-Reinhold & Platnick 1986; Huber 2011), as it did clearly not fit into any of the other two species groups.



**Fig. 16.** Known distribution of the *Panjange lanthana* group.

With the new species from the Philippines described below, the *lanthana* group can finally be characterized based on several species, and the emended diagnosis below takes account of these new species.

### Diagnosis

Distinguished from closest known relatives (other species of *lanthana* group) by absence of processes arising from near male PME (cf. fig. 441 in Huber 2011), by presence of clearly visible AME, and by morphology of male palp (cf. figs 436, 437 in Huber 2011; procurus with two highly distinctive sclerites hinged against proximal part; appendix with simple weakly sclerotized tip). From three species of the *lanthana* group (*Pa. malagos* Huber sp. nov.; *Pa. casaroro* Huber sp. nov.; *Pa. camiguin* Huber sp. nov.) also by symmetric palps; from another three species of the *lanthana* group (*Pa. isarog* Huber sp. nov.; *Pa. dinagat* Huber sp. nov.; *Pa. marilog* Huber sp. nov.) also by unmodified male clypeus and by epigynal scape directed toward posterior (fig. 439 in Huber 2011); from *Pa. hamiguitan* Huber sp. nov. also by much shorter palpal segments and epigynal scape.

### New material examined

PHILIPPINES: Luzon, Camarines Sur Province: 2 ♂♂, 4 ♀♀ in ZFMK (Ar12997) and 1 ♂, 1 ♀ in MSU-IIT, Mt. Isarog, W slope (13.664°N, 123.34–123.35°E), ~600–900 m a.s.l., forest, on leaves, 23 Feb. 2014 (B.A. Huber); 6 juvs in pure ethanol in ZFMK (Phi 224), same data.

### Natural history

All specimens were found in a shady ravine, with their domed webs connected to the undersides of green leaves among the vegetation, about 1–2 m above the ground.

### Distribution

Known from two localities on southern Luzon Island (Fig. 16).

### *Panjange malagos* Huber sp. nov.

[urn:lsid:zoobank.org:act:00D7154A-7034-4494-AE2D-026298207059](https://zoobank.org/act:00D7154A-7034-4494-AE2D-026298207059)

Figs 5, 17–23

### Diagnosis

Easily distinguished from closest known relatives (*Pa. casaroro* Huber sp. nov.; *Pa. camiguin* Huber sp. nov.) by short male eye stalks (Fig. 17), and by morphology of male palps (Figs 18–21; symmetric modifications of trochanter and femur; asymmetric shapes of procursi); from *Pa. casaroro* Huber sp. nov. also by simple epigynal scape without pair of semi-transparent lobes (Fig. 22); from *Pa. camiguin* Huber sp. nov. also by absence of strong transversal sclerite in female internal genitalia (Fig. 23).

### Etymology

The species name is derived from the type locality; noun in apposition.

### Type material

PHILIPPINES: holotype ♂, in ZFMK (Ar 12998), Mindanao, Davao del Sur Province, Malagos Watershed (7.184°N, 125.415°E), 390 m a.s.l., forest along river, on leaves, 14 Feb. 2014 (B.A. Huber, E. Mondejar).

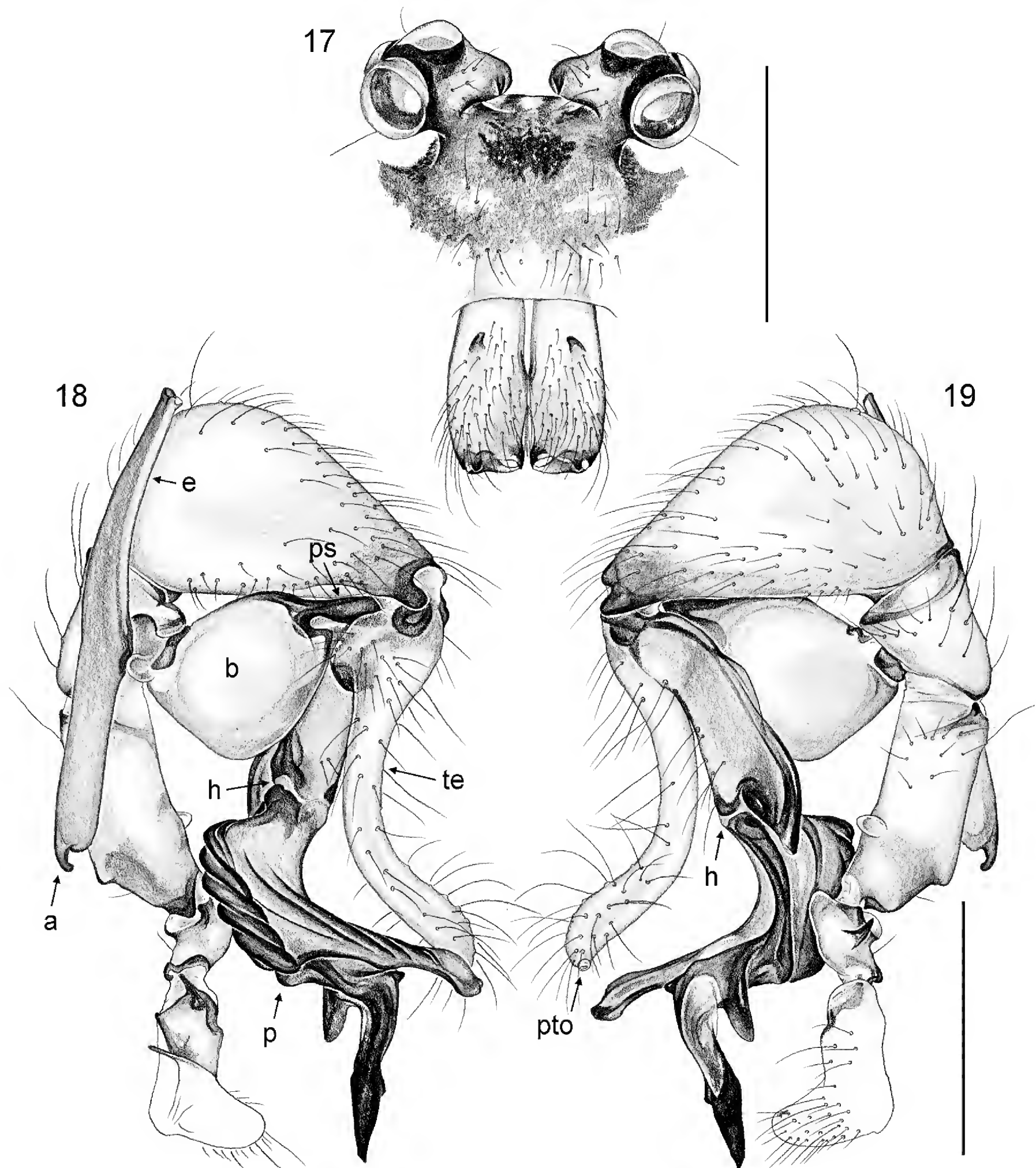
### Other material examined

PHILIPPINES: 1 ♂, 2 ♀♀ in ZFMK (Ar 12999) and 1 ♀ in MSU-IIT, same data as holotype; 1 ♀ in pure ethanol, in ZFMK (Phi 259), same data.

## Description

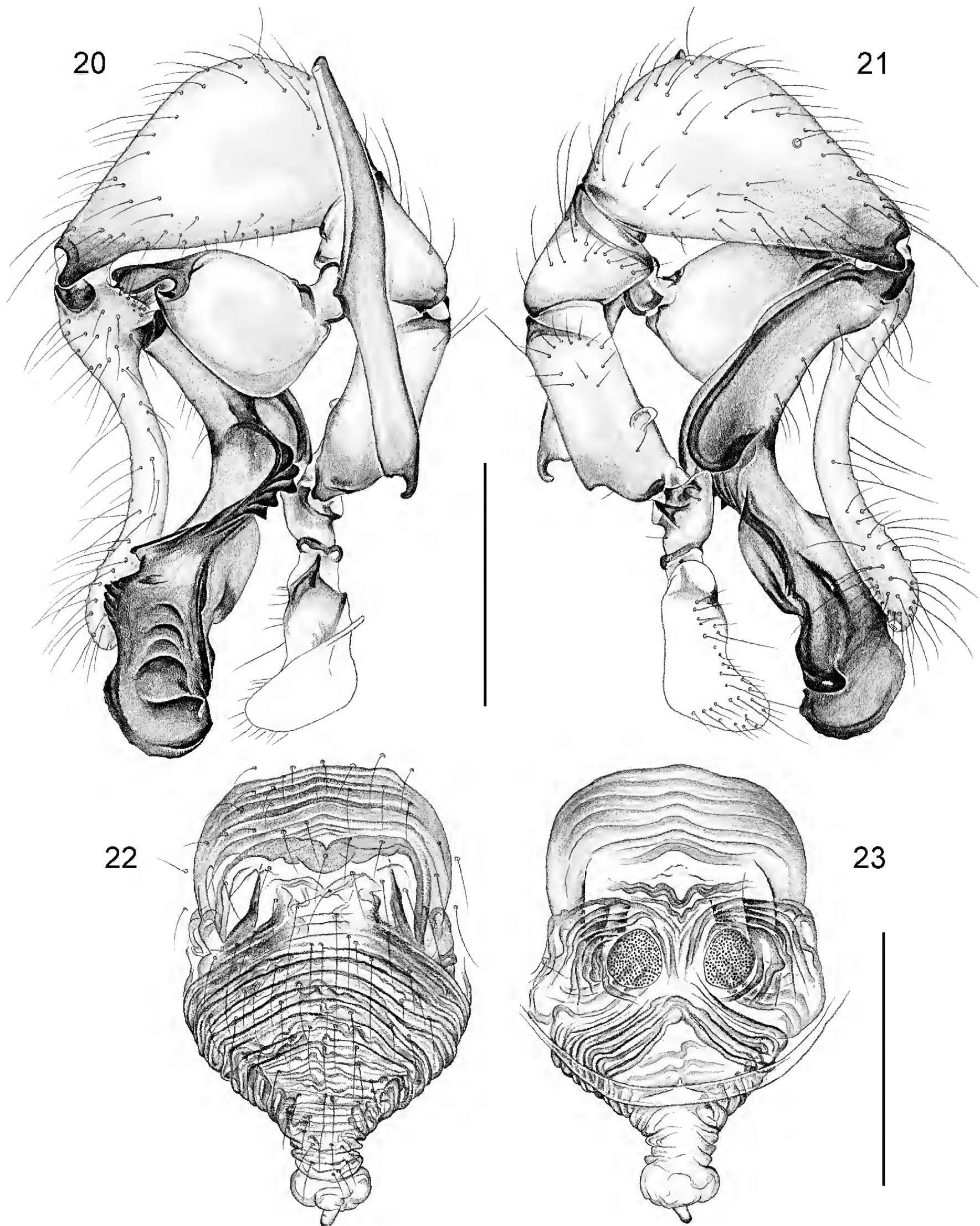
### Male (holotype)

MEASUREMENTS. Total body length 4.6, carapace width 0.9. Leg 1: 41.3 (9.7 + 0.4 + 9.8 + 19.4 + 2.0), tibia 2: 6.0, tibia 3: 3.2, tibia 4: 4.9; tibia 1 L/d: 110. Distance PME–PME 270  $\mu$ m, diameter PME 120  $\mu$ m, distance PME–ALE ~40  $\mu$ m; AME absent.



**Figs 17–19.** *Panjange malagos* Huber sp. nov. (ZFMK, Ar 12999). 17. Male prosoma and chelicerae, frontal view. 18–19. Left male palp, prolateral and retrolateral views. Abbreviations: a = appendix; b = genital bulb; e = embolus; h = hinge; p = procurus; ps = proximal bulbal sclerite; pto = palpal tarsal organ; te = tarsal elongation. Scale bars = 0.5 mm.

COLOR. Carapace pale ochre yellow with indistinct posterior median mark, ocular area and clypeus brown, black mark in AME area; sternum whitish; legs ochre-yellow with dark brown patellae and tibia-metatarsus joints; abdomen ochre-gray, with black marks dorsally, monochromous ventrally.



**Figs 20–23.** *Panjange malagos* Huber sp. nov. (ZFMK, Ar 12999). **20–21.** Right male palp, prolateral and retrolateral views. **22–23.** Cleared female genitalia, ventral and dorsal views. Scale bars = 0.5 mm.

**BODY.** Habitus as in Fig. 5; ocular area raised, each triad on short stalk, medially with pointed process directed toward frontal and ventral (Fig. 17); carapace without median furrow; clypeus unmodified; sternum wider than long (0.65/0.55), unmodified.

**CHELICERAE.** As in Fig. 17, with simple pair of weakly sclerotized processes in rather frontal position, without modified hairs; without stridulatory ridges.

**PALPS.** As in Figs 18–21; proximal segments symmetric in shape but slightly larger on left side (e.g., length and diameter of right tibia about 95–97% of left tibia); coxa with strong ventro-distal rim but otherwise unmodified; trochanter with pointed retrolateral apophysis and rounded ventral hump; femur with dorsal hump and weakly sclerotized semitransparent process retrolatero-ventrally; tarsus with long whitish elongation with terminal tarsal organ; procursi of left and right palps strongly different, distal part of procurus clearly hinged in left palp, not hinged in right palp; bulb slightly smaller in right palp, with long processes extending in opposite directions (dorsal embolus; ventral appendix) almost symmetric (slightly longer in left palp).

**LEGS.** Without spines and curved hairs; few vertical hairs; retrolateral trichobothrium on tibia 1 at 3%; prolateral trichobothrium absent on tibia 1, present on other tibiae; tarsus 1 with > 20 pseudosegments, only distally fairly distinct.

**Male** (variation)

Not seen. Tibia 1 missing in other male.

**Female**

In general similar to male but eye triads on low humps and closer together (distance PME–PME 210 µm). Tibia 1 in 3 females: 6.9, 7.0, 7.9. Epigynum large elongate plate, anterior part weakly sclerotized, with symmetric or at most slightly asymmetric internal structures visible through cuticle; posterior part orange, with extensible scape with distinct transversal folds and small median process (“knob”) at tip (Fig. 22); internal genitalia as in Fig. 23.

**Natural history**

The spiders were found in very low abundance on the undersides of leaves about 50–200 cm above the ground in a disturbed part of the forest.

**Distribution**

Known from type locality on Mindanao Island only (Fig. 16).

*Panjange casaroro* Huber sp. nov.

[urn:lsid:zoobank.org:act:D6FF36FF-D69F-4F92-919F-82F423701E71](https://doi.org/10.2307/26462370)

Figs 6–7, 24–34

**Diagnosis**

Easily distinguished from closest known relatives (*Pa. malagos* Huber sp. nov.; *Pa. camiguin* Huber sp. nov.) by morphology of male palps (Figs 24–27; symmetric modifications of trochanter and femur; asymmetric shapes of procursi), and by pair of semi-transparent lobes on epigynal scape (Figs 29, 33). From most congeners (except *Pa. camiguin* Huber sp. nov.) also by very long eye stalks and contiguous tips of male ocular processes (Fig. 28); from *Pa. camiguin* Huber sp. nov. also by proximally unmodified male chelicerae (densely covered with small scales in *Pa. camiguin* Huber sp. nov.; cf. Fig. 47) and by small process between eye stalks (Fig. 28).

**Etymology**

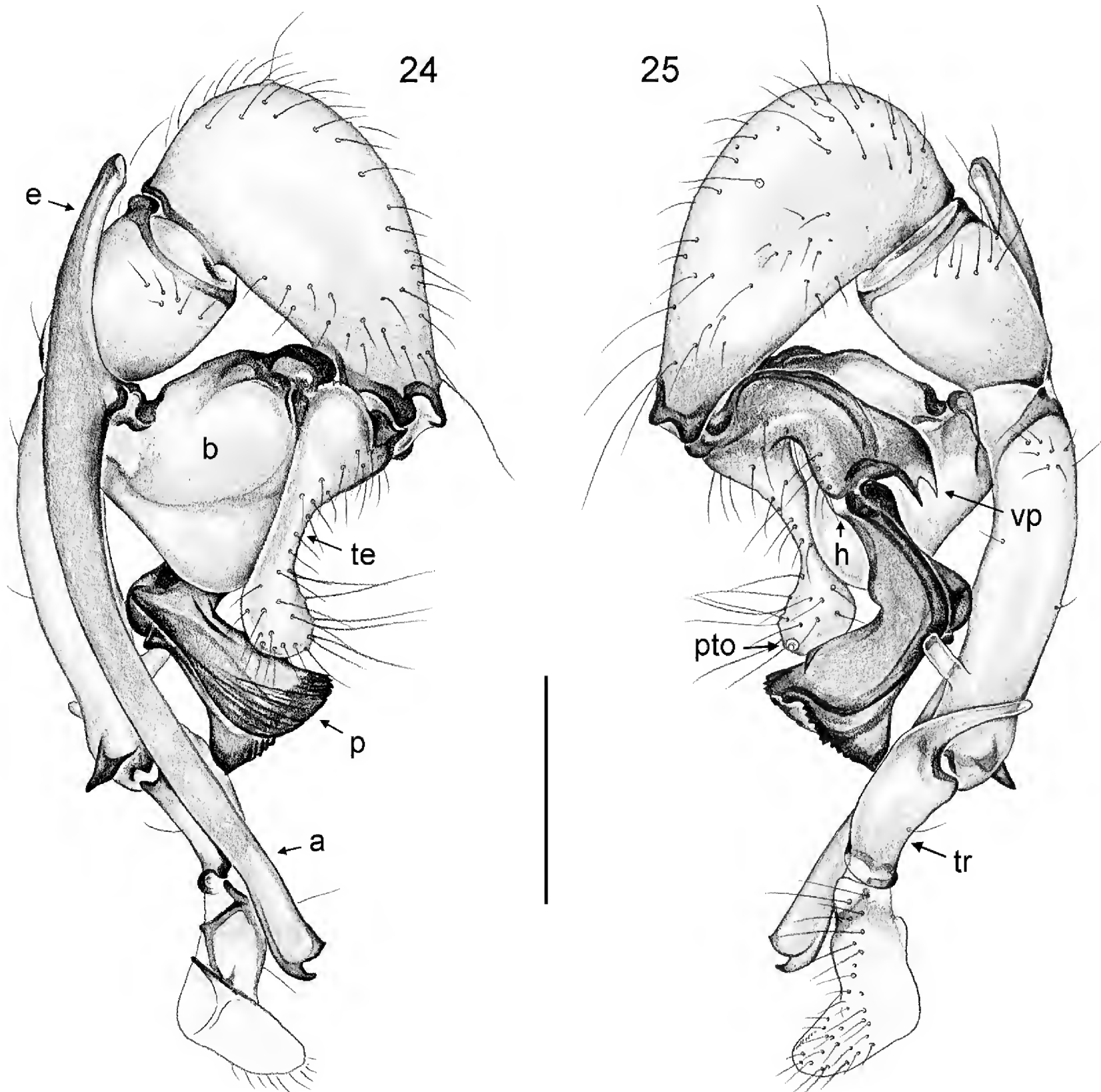
The species name is derived from the type locality; noun in apposition.

**Type material**

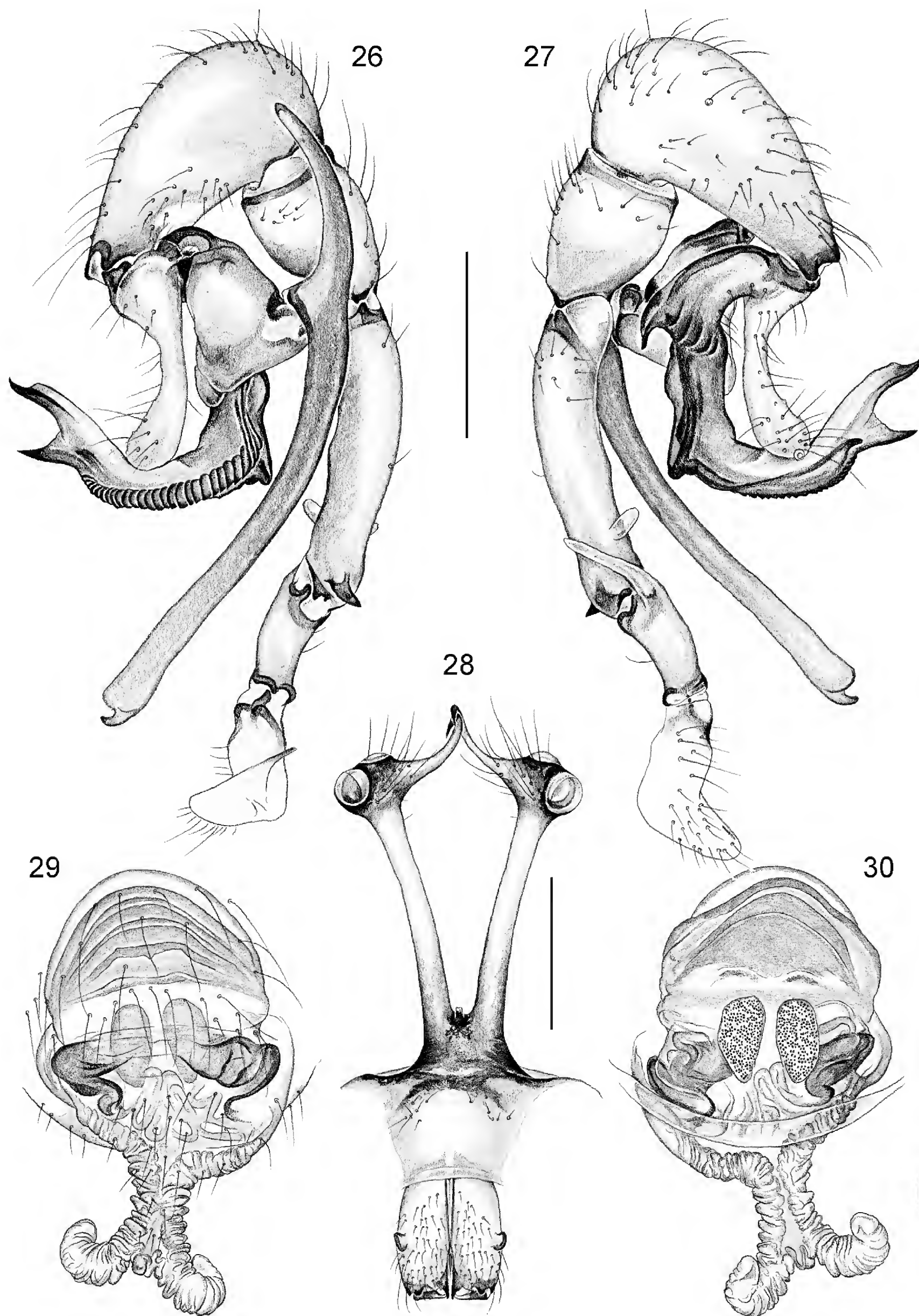
PHILIPPINES: holotype ♂, in ZFMK (Ar 13000), Negros Island, Negros Oriental Province, Casaroro Falls (9.281°N, 123.208°E), 550 m a.s.l., forest along river below waterfall, on leaves, 10 Mar. 2014 (B.A. Huber).

**Other material examined**

PHILIPPINES: 1 ♂, 3 ♀♀ in ZFMK (Ar 13001) and 1 ♂, 1 ♀ in MSU-IIT, same data as holotype; 1 ♀, 1 juv. in pure ethanol, in ZFMK (Phi 187), same data.



**Figs 24–25.** *Panjange casaroro* Huber sp. nov. (ZFMK, Ar 13001), left male palp, prolateral and retrolateral views. Abbreviations: a = appendix; b = genital bulb; e = embolus; h = hinge; p = procurus; pto = palpal tarsal organ; te = tarsal elongation; tr = trochanter; vp = ventral process. Scale bar = 0.5 mm.



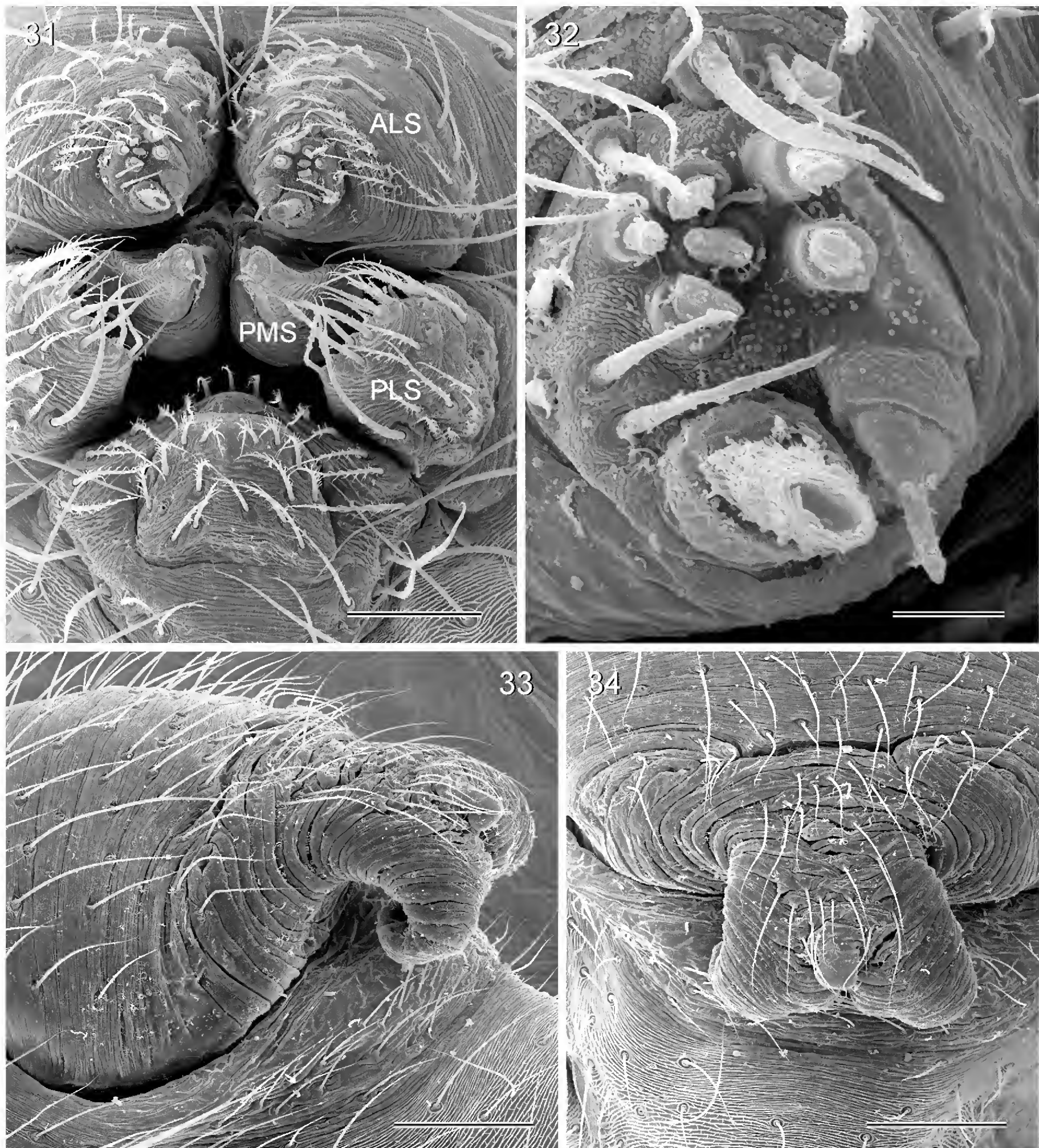
**Figs 26–30.** *Panjange casaroro* Huber sp. nov. (ZFMK, Ar 13001). **26–27.** Right male palp, prolateral and retrolateral views. **28.** Male prosoma and chelicerae, frontal view. **29–30.** Cleared female genitalia, ventral and dorsal views. Scale bars = 0.5 mm.



**Description**

**Male (holotype)**

MEASUREMENTS. Total body length 4.8, carapace width 1.0. Leg 1: 39.2 (9.2 + 0.5 + 9.4 + 18.9 + 1.2), tibia 2: 5.6, tibia 3: 3.2, tibia 4: 4.9; tibia 1 L/d: 106. Distance PME–PME 420  $\mu$ m, diameter PME 105  $\mu$ m, distance PME–ALE  $\sim$ 30  $\mu$ m; AME absent.



**Figs 31–34.** *Panjange casaroro* Huber sp. nov., SEM micrographs (ZFMK, Ar 13001). **31.** Female spinnerets. **32.** Female ALS. **33–34.** Epigynum and scape. **33.** Lateral (slightly posterior) view. **34.** Ventral view. Abbreviations: ALS, anterior lateral spinneret; PLS = posterior lateral spinneret; PMS = posterior median spinneret. Scale bars: 31 = 60  $\mu$ m; 32 = 10  $\mu$ m; 33–34 = 100  $\mu$ m.

**COLOR.** Carapace and clypeus pale ochre to whitish, only base of eye stalks dark; sternum whitish; legs ochre-yellow with dark brown patellae and tibia-metatarsus joints; abdomen pale gray, with black marks dorsally, monochromous ventrally.

**BODY.** Habitus as in Figs 6–7; ocular area raised, triads on long stalks with further distal processes whose contiguous tips seem to form a functional unit (Fig. 28); with small process between eye stalks; carapace without median furrow; clypeus unmodified; sternum wider than long (0.65/0.55), unmodified.

**CHELICERAE.** As in Fig. 28, with pair of simple, weakly sclerotized lateral processes, without modified hairs; without stridulatory ridges.

**PALPS.** As in Figs 24–27; proximal segments symmetric in shape but slightly larger on left side (e.g., length and diameter of right tibia about 90–95% of left tibia); coxa with strong ventro-distal rim but otherwise unmodified; trochanter with long weakly sclerotized retrolateral process directed toward dorsal; femur with weakly sclerotized finger-shaped process retrolatero-ventrally and more heavily sclerotized apophysis prolatero-dorsally; tibia with retrolateral trichobothrium in rather proximal position; tarsus with long whitish elongation, distally more strongly widened (club-shaped) in left palp; procursi of left and right palps strongly different, in each case with ventral process arising from proximal part (simple in right palp; bifid in left palp); distal part of procurus clearly hinged in left palp, not hinged in right palp; bulb much smaller in right palp, long processes extending in opposite directions (dorsal embolus; ventral appendix) almost symmetric (slightly longer in left palp).

**LEGS.** Without spines and curved hairs; few vertical hairs; retrolateral trichobothrium on tibia 1 at 3%; prolateral trichobothrium absent on tibia 1, present on other tibiae; tarsus 1 with > 20 pseudosegments, only distally fairly distinct.

**Male** (variation)

Tibia 1 in other male: 9.5 (missing in third male).

**Female**

In general similar to male but eye triads on low humps and much closer together (distance PME–PME 265 µm); with dark mark in place of AME. Tibia 1 in 4 females: 6.7, 7.0, 7.1, 7.4. Epigynum mostly weakly sclerotized, with apparently slightly asymmetric internal structures visible through cuticle; distinctive scape with small median process at tip and two long extensible projections curved toward dorsal (Figs 29, 33, 34); internal genitalia as in Fig. 30.

**Natural history**

The spiders were found on the undersides of large leaves about 50–100 cm above the ground.

**Distribution**

Known from type locality on Negros Island only (Fig. 16).

*Panjange camiguin* Huber sp. nov.

[urn:lsid:zoobank.org:act:A8245A4A-D792-4023-8E50-0922A9C29FD6](https://zoobank.org/urn:lsid:zoobank.org:act:A8245A4A-D792-4023-8E50-0922A9C29FD6)

Figs 8–10, 35–63

**Diagnosis**

Easily distinguished from closest known relatives (*Pa. malagos* Huber sp. nov.; *Pa. casaroro* Huber sp. nov.) by morphology of male palps (Figs 38–39; symmetric modifications of trochanter and femur; asymmetric shapes of procursi; Figs 41–44), by proximally modified male chelicerae (densely covered

with small scales; Fig. 47), and by strong internal sclerite in female genitalia (Fig. 37). From most congeners (except *Pa. casaroro* Huber sp. nov.) also by contiguous tips of male ocular processes (Figs 35, 45, 48–49); from *Pa. casaroro* Huber sp. nov. also by absence of process between eye stalks (Fig. 35), and by simple epigynal scape (Fig. 36; not with two distal lobes).

### Etymology

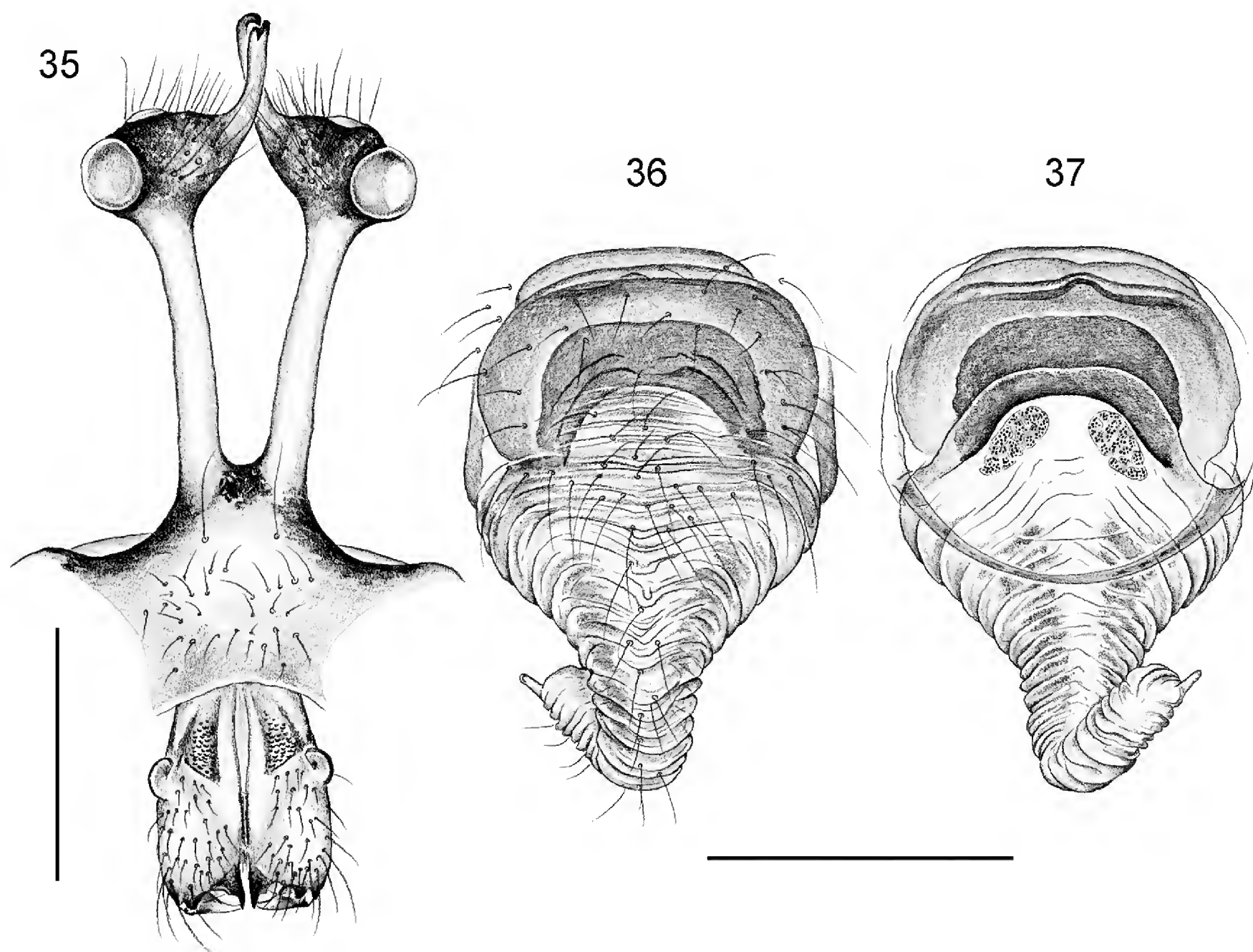
The species name is derived from the type locality; noun in apposition.

### Type material

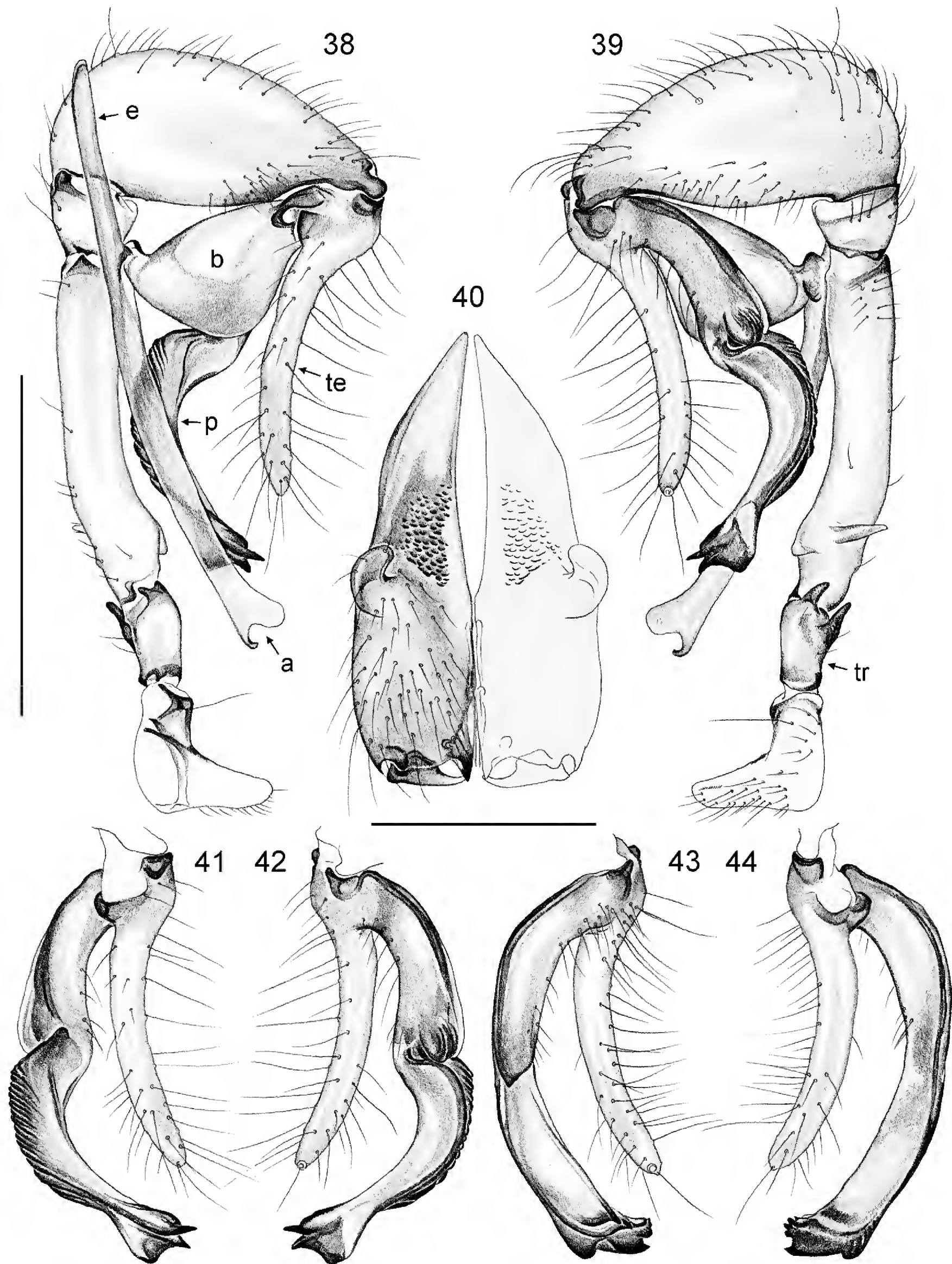
PHILIPPINES: holotype ♂, in ZFMK (Ar 13002), Camiguin Island, Katibawasan Falls (9.215°N, 124.720°E), 300 m a.s.l., on leaves, 19 Feb. 2014 (B.A. Huber, P.N. Banaag).

### Other material examined

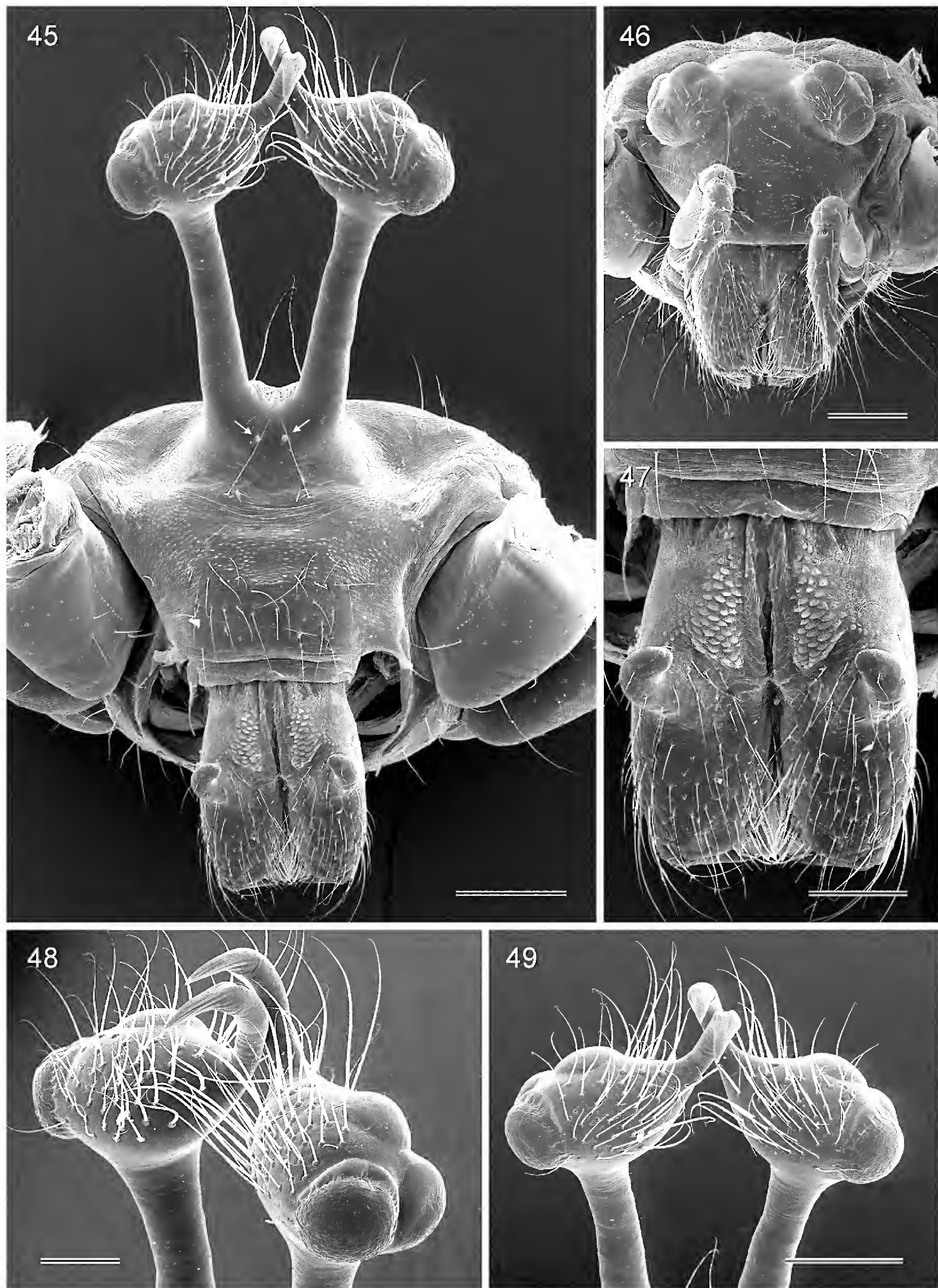
PHILIPPINES: Camiguin Island: 7 ♂♂, 17 ♀♀, 1 juv. in ZFMK (Ar 13003, 13004) and 1 ♂, 1 ♀ in MSU-IIT, same data as holotype; 2 ♀♀, 2 juvs in pure ethanol, in ZFMK (Phi 235), same data; 2 ♂♂, 2 ♀♀, 2 juvs in ZFMK (Ar 13005) and 1 ♂, 1 ♀ in MSU-IIT, all poorly preserved, same locality, 5–6 May 2014 (E.P. Mondejar); 2 ♂♂, 7 ♀♀, 1 juv. in ZFMK (Ar 13006), Mt. Hibok Hibok (9.196°N, 124.692°E), 600 m a.s.l., on leaves, 18 Feb. 2014 (B.A. Huber, P.N. Banaag); 2 ♀♀, 2 juvs in pure ethanol, in ZFMK (Phi 241), same data. Bohol Island: 2 ♂♂, 5 ♀♀ in ZFMK (Ar 13007), near Loboc, above Loboc River (~9.655°N, 124.015°E), ~250 m a.s.l., forest near caves, 5 Mar. 2014 (B.A. Huber);



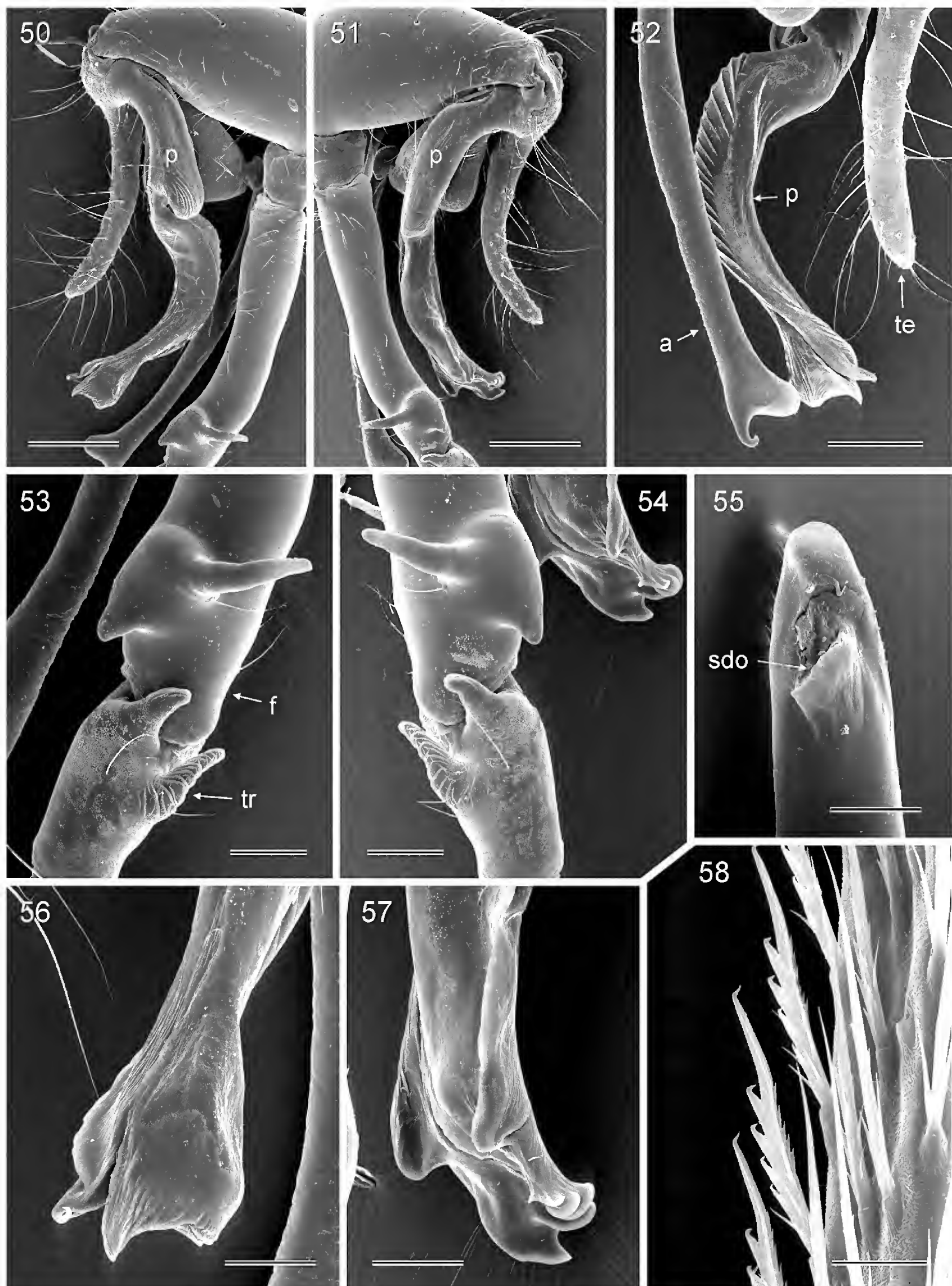
**Figs 35–37.** *Panjange camiguin* Huber sp. nov. (ZFMK, Ar 13003, 13004). **35.** Male prosoma and chelicerae, frontal view. **36–37.** Cleared female genitalia, ventral and dorsal views. Scale bars = 0.5 mm.



**Figs 38–44.** *Panjange camiguin* Huber sp. nov. (ZFMK, Ar 13003). **38–39.** Left male palp, prolateral and retrolateral views. **40.** Male chelicerae, frontal view. **41–42.** Left male tarsus and procurus, prolateral and retrolateral views. **43–44.** Right male tarsus and procurus, retrolateral and prolateral views. Abbreviations: a = appendix; b = genital bulb; e = embolus; p = procurus; te = tarsal elongation; tr = trochanter. Scale bars: 38–39, 41–44 = 1 mm; 40 = 0.3 mm.

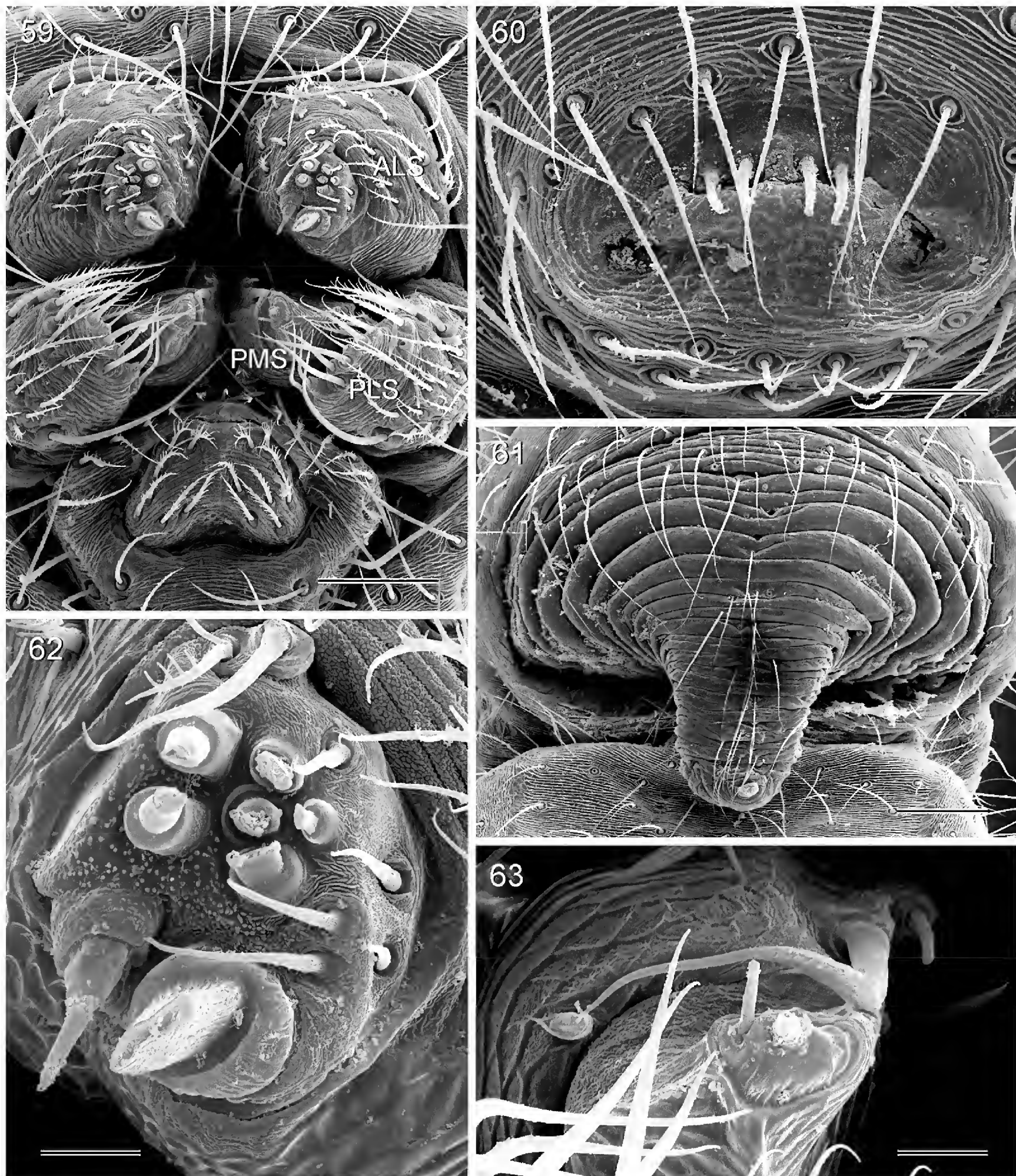


**Figs 45–49.** *Panjange camiguin* Huber sp. nov., SEM micrographs (ZFMK, Ar 13003, 13004). **45–46.** Male and female prosomata, frontal views (arrows point at tiny AME remnants). **47.** Male chelicerae. **48–49.** Male eye triads and ocular processes, oblique frontal and frontal views. Scale bars: 45–46, 49 = 200  $\mu$ m; 47–48 = 100  $\mu$ m.



**Figs 50–58.** *Panjange camiguin* Huber sp. nov., SEM micrographs (ZFMK, Ar 13003, 13004). **50–51.** Left and right male palps, retrolateral views. **52.** Left procurus and appendix, prolateral view. **53–54.** Left and right male palpal trochanters and femora proximally, retrolateral views. **55.** Tip of embolus. **56–57.** Left and right procurus tips, retrolateral views. **58.** Comb-hairs on female tarsus 4. Abbreviations: a = appendix; f = femur; p = procurus; sdo = sperm duct opening; te = tarsal elongation; tr = trochanter. Scale bars: 50–51 = 300  $\mu$ m; 52 = 200  $\mu$ m; 53–54 = 100  $\mu$ m; 55 = 30  $\mu$ m; 56–57 = 80  $\mu$ m; 58 = 20  $\mu$ m.

1 ♀, 3 juvs in pure ethanol, in ZFMK (Phi 199), same data; 1 ♀ with 8 hymenopteran parasites and 2 juveniles emerged from same egg sac, in pure ethanol in ZFMK (Phi 291), same data (Fig. 8); 1 ♂, 4 ♀♀, 1 juv. in ZFMK (Ar 13008), Rajah Sikatuna (Magsaysay Park) (9.705°N, 124.123°E), 430 m a.s.l., forest, on leaves, 6 Mar. 2014 (B.A. Huber); 4 juvs in pure ethanol in ZFMK (Phi 194), same data; 5 ♂♂, 11 ♀♀, 34 juvs in ZFMK (Ar 15064) and 2 ♂♂, 2 ♀♀ in MSU-IIT, Bilar, Barangay Riverside (~9.705°N, 12.125°E), 15 Jun. 2015 (M.R.B. Dacar).



**Figs 59–63.** *Panjange camiguin* Huber sp. nov., SEM micrographs (ZFMK, Ar 13003, 13004). **59.** Female spinnerets. **60.** Male gonopore. **61.** Epigynum and scape, ventral view. **62.** Female ALS. **63.** Female PMS. Abbreviations: ALS = anterior lateral spinneret; PLS = posterior lateral spinneret; PMS = posterior median spinneret. Scale bars: 59 = 60 µm; 60 = 30 µm; 61 = 100 µm; 62–63 = 10 µm.

### **Assigned tentatively**

PHILIPPINES, Bohol Island: 2 ♂♂, 4 juvs in ZFMK (Ar 15065) and 1 ♂ in MSU-IIT, Garcia Hernandez, Barangay Datag (~9.719°N, 124.262°E), 8 Jun. 2015 (M.R.B. Dacar); 3 ♂♂, 4 ♀♀, 4 juvs in ZFMK (Ar 15066) and 1 ♂, 1 ♀ in MSU-IIT, Valencia, Barangay Marawis (9.723°N, 124.202°E), 10–11 Jun. 2015 (M.B.R. Dacar); 2 ♂♂, 8 ♀♀, 5 juvs in ZFMK (Ar 15067) and 1 ♂, 1 ♀ in MSU-IIT, Sierra Bullones, Barangay Nan-od (~9.748°N, 124.264°E), 4–5 Jun. 2015 (M.R.B. Dacar).

### **Description**

#### **Male (holotype)**

MEASUREMENTS. Total body length 5.0, carapace width 1.0. Leg 1: 43.2 (9.8 + 0.5 + 9.9 + 21.1 + 1.9), tibia 2: 6.1, tibia 3: 3.1, tibia 4: 5.0; tibia 1 L/d: 103. Distance PME–PME 355 µm, diameter PME 125 µm, distance PME–ALE ~35 µm; with tiny AME lenses barely visible in dissecting microscope, diameter ~10 µm (Fig. 45).

COLOR. Carapace pale ochre with darker triangular mark posteriorly, pair of dark marks lateral of base of eye stalks, and median mark in AME area; clypeus without pattern; sternum whitish; legs ochre-yellow with dark brown patellae and tibia-metatarsus joints; abdomen pale gray, with black marks dorsally, monochromous ventrally.

BODY. Habitus as in Figs 9–10; ocular area raised, triads on long additional stalks with further distal processes whose contiguous tips seem to form a functional unit (Figs 35, 45, 48–49); without process between eye stalks; carapace without median furrow; clypeus unmodified; sternum wider than long (0.70/0.50), unmodified.

CHELICERAE. As in Fig. 47, with pair of curved, weakly sclerotized lateral processes, proximally densely covered with small scales; without modified hairs; without stridulatory ridges.

PALPS. As in Figs 38–39, 50–51; proximal segments symmetric in shape and apparently also in size (Figs 53–54); coxa with strong ventro-distal rim but otherwise unmodified; trochanter with distinctive pair of apophyses (retrolateral and dorsal; Figs 53, 54); femur with weakly sclerotized retrolateral process directed toward dorsal and short ventral process directed toward proximal (Figs 53, 54); patella very small; tibia large; tarsus with long whitish elongation; procursi of left and right palps slightly but clearly different, distal part of procurus hinged in left palp, not hinged in right palp (Figs 41–44); bulb symmetric in shape, with long processes extending in opposite directions (dorsal embolus; ventral appendix), apparently slightly longer in left palp.

LEGS. Without spines and curved hairs; few vertical hairs; retrolateral trichobothrium on tibia 1 at 3%; prolateral trichobothrium absent on tibia 1, present on other tibiae; tarsus 1 with > 20 pseudosegments, only distally fairly distinct.

#### **Male (variation)**

Tibia 1 in 11 other males: 8.6–10.1 (mean 9.5). Males from the three eastern sites on Bohol Island (Datag, Marawis, Nan-od) differ slightly but consistently from other specimens in the tip of the right procurus that has a distinct retrolateral process. Specimens from these localities are therefore assigned tentatively.

#### **Female**

In general similar to male but eye triads on low humps and much closer together (distance PME–PME 260 µm), without AME remnants (Fig. 46); posterior mark on carapace smaller, often medially divided; dark abdomen spots in some specimens very indistinct or even absent. Tibia 1 in 32 females: 6.4–8.2 (mean



7.1). Epigynum apparently symmetric, mostly weakly sclerotized, with strong internal transversal sclerite visible through cuticle; extensible scape with strong transversal folds, laterally light brown to orange, with small median process at tip (Figs 36, 61); internal genitalia as in Fig. 37, also apparently symmetric.

### Natural history

The spiders were found on the undersides of large leaves to which they attach fairly dense but barely visible sheets of silk. One female was collected on 5 Mar. 2014 with a parasitized egg sac from which all eggs hatched on 12 Mar. 2014 (two spiders and eight wasps).

### Distribution

Known from Camiguin and Bohol Islands (Fig. 16).

### *Panjange hamiguitan* Huber sp. nov.

[urn:lsid:zoobank.org:act:C44C7291-5943-45C1-AAC1-F6B684836BBD](https://zoobank.org/urn:lsid:zoobank.org:act:C44C7291-5943-45C1-AAC1-F6B684836BBD)

Figs 64–68

### Diagnosis

Easily distinguished from known congeners by extremely elongated male palpal elements and female epigynal scape (Figs 64–65, 67).

### Etymology

The species name is derived from the type locality; noun in apposition.

### Type material

PHILIPPINES: holotype ♂, in ZFMK (Ar 13009), Mindanao, Davao Oriental, Mount Hamiguitan Wildlife Sanctuary (access Governor Generoso), “site 1” (9.6463°N, 126.1442°E), 250 m a.s.l., 12 Feb. 2015 (M.A. Responde).

### Other material examined

PHILIPPINES, Mindanao, Davao Oriental: 1 ♀, 2 juvs in ZFMK (Ar 13010) and 1 ♀ in MSU-IIT, same data as holotype; 1 ♀, 1 juv. in ZFMK (Ar 13011), Mount Hamiguitan Wildlife Sanctuary (access Governor Generoso), “site 2” (9.6497°N, 126.1487°E), 360 m a.s.l., 13 Feb. 2015 (M.A. Responde); 1 ♀, 1 juv. in ZFMK (Ar 13012), Mount Hamiguitan Wildlife Sanctuary (access Governor Generoso), “site 3” (9.6569°N, 126.1559°E), 580 m a.s.l., 13 Feb. 2015 (M.A. Responde).

### Description

#### Male (holotype)

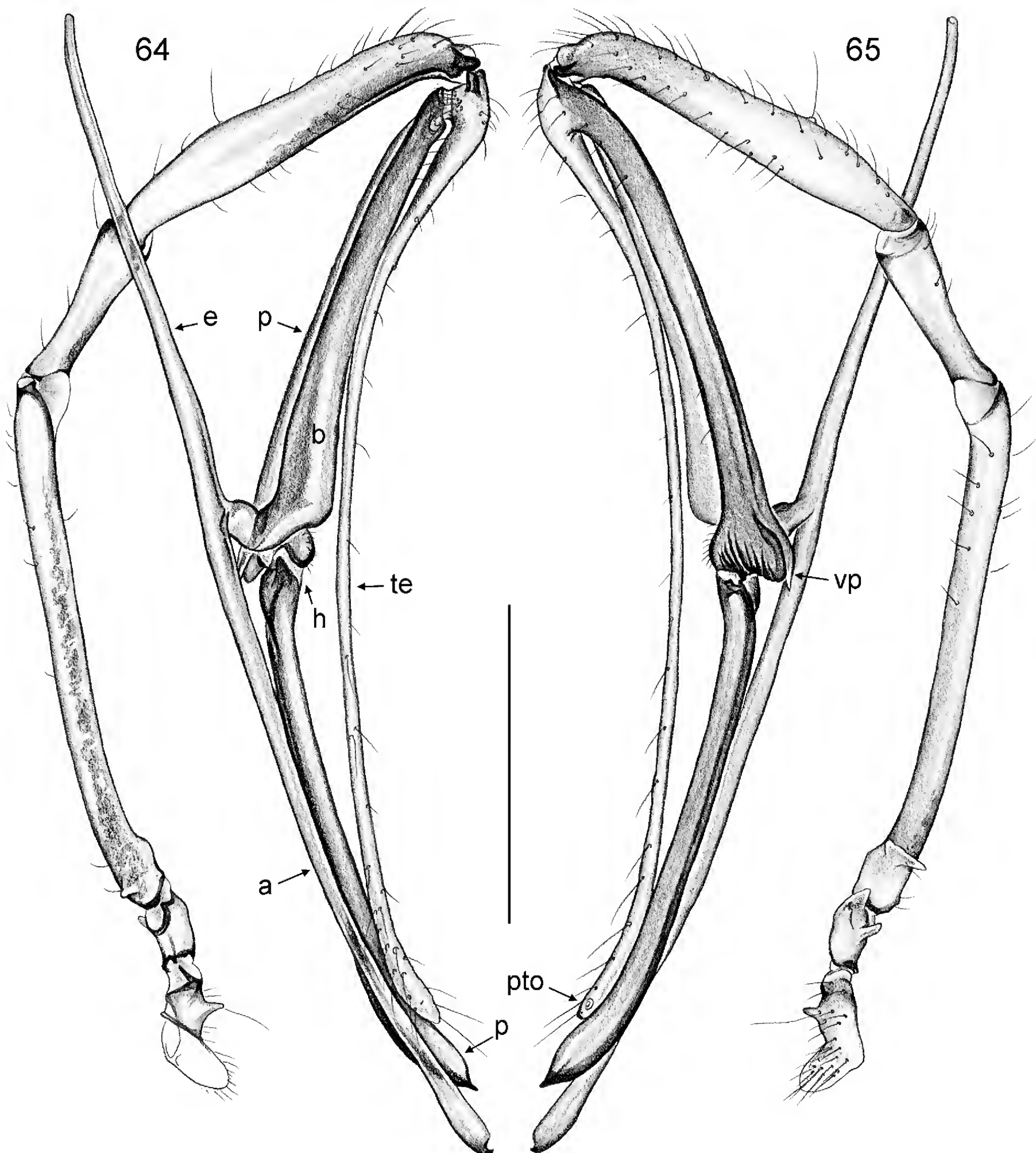
MEASUREMENTS. Total body length 5.1, carapace width 0.9. Leg 1: ~33.3 (7.9 + 0.4 + 7.8 + 15.7 + ~1.5), tibia 2: 4.9, tibia 3: 2.8, tibia 4: 4.3; tibia 1 L/d: 99. Distance PME–PME 195 µm, diameter PME 95 µm, distance PME–ALE ~60 µm; AME absent.

COLOR. Carapace pale ochre-yellow with pair of light brown marks, ocular area dark brown, with black marks in place of AME, clypeus pale ochre to whitish; sternum whitish; legs pale ochre-yellow with dark brown patellae and tibia-metatarsus joints; abdomen pale gray, with many black marks dorsally and laterally; ventrally with pair of small dark marks near book-lung covers.

BODY. Habitus similar to *Pa. casaroro* Huber sp. nov. and *Pa. camiguin* Huber sp. nov. (cf. Figs 6, 9); ocular area raised, triads on additional stalks with further weakly sclerotized distal processes directed toward each other (Fig. 66); carapace without median furrow; clypeus unmodified; sternum wider than long (0.56/0.46), unmodified.

CHELICERAE. As in Fig. 66, with pair of simple, weakly sclerotized frontal processes slightly directed upwards, without modified hairs; without stridulatory ridges.

PALPS. As in Figs 64–65; all elements symmetrical; all elements distal of trochanter extremely elongated; coxa with distinct ventral apophysis; trochanter with two weakly sclerotized retrolateral processes; femur with weakly sclerotized bifid retrolateral process proximally; tarsus with extremely slender elongation,



**Figs 64–65.** *Panjange hamiguitan* Huber sp. nov. (ZFMK, Ar 13009), left male palp, prolateral and retrolateral views. Abbreviations: a = appendix; b = genital bulb; e = embolus; h = hinge; p = procurus; pto = palpal tarsal organ; te = tarsal elongation; vp = ventral process. Scale bar = 1 mm.

with tarsal organ near tip; procurus consisting of two hinged parts; proximal part distally widened, with small pointed ventral process; distal part very simple; bulb very thin and long, with long processes extending in opposite directions (dorsal embolus; ventral appendix).

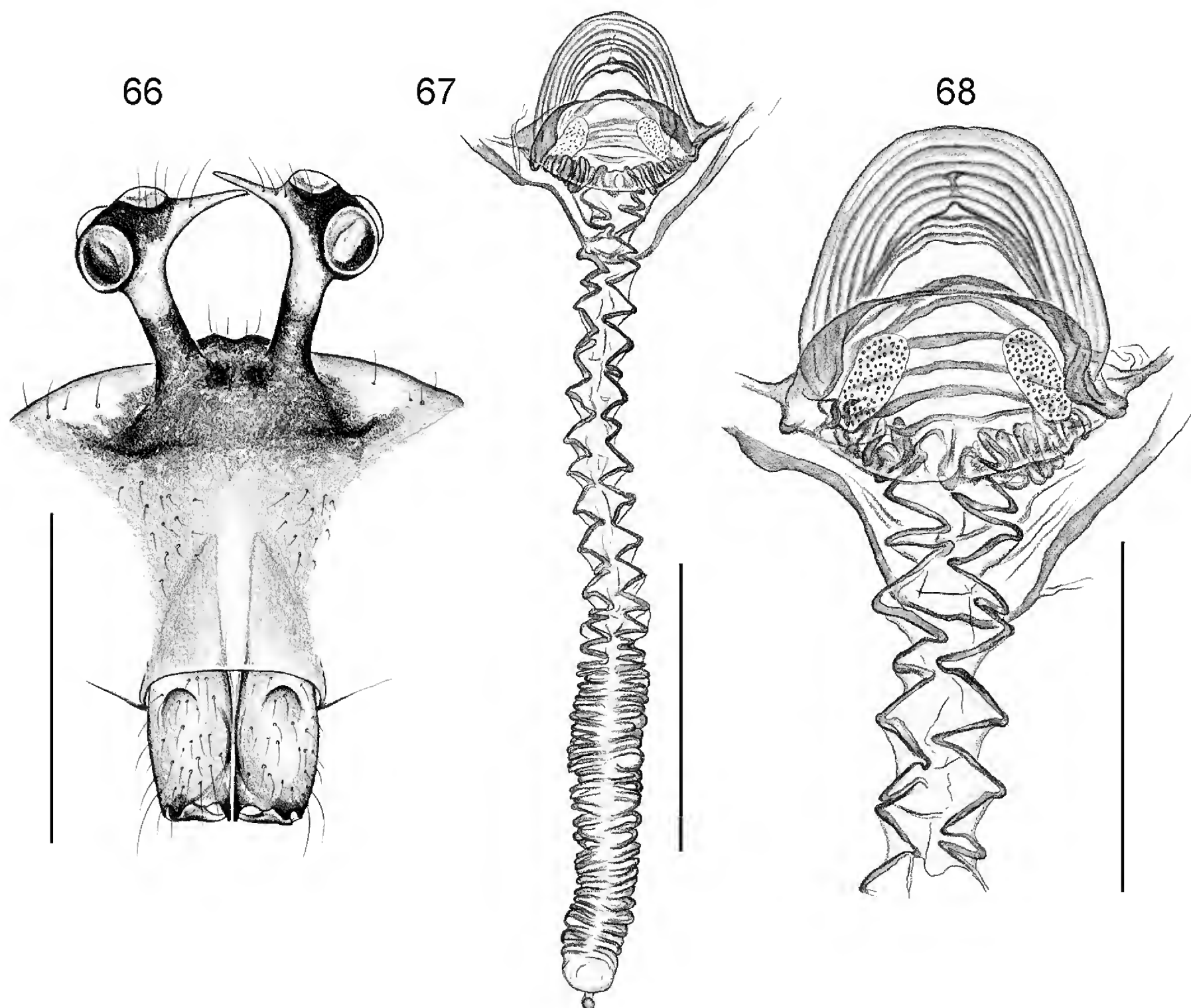
LEGS. Without spines and curved hairs; few vertical hairs; retrolateral trichobothrium on tibia 1 at 3%; prolateral trichobothrium absent on tibia 1, present on other tibiae.

### Female

In general similar to male but eye triads on low humps, ocular area with narrow transversal dark mark including black marks in place of AME. Tibia 1: 6.8 (missing in other females). Epigynum pale, weakly sclerotized, with very long strongly folded and extensible scape (Fig. 67); internal genitalia as in Fig. 68.

### Distribution

Known from type locality on Mindanao only (Fig. 16).



**Figs 66–68.** *Panjange hamiguitan* Huber sp. nov. (ZFMK, Ar 13009, 13012). **66.** Male prosoma and chelicerae, frontal view. **67.** Cleared female genitalia, dorsal view (proximal part of scape partly extended). **68.** Detail of Fig. 67. Scale bars: 66–67 = 0.5 mm; 68 = 0.3 mm.

***Panjange isarog* Huber sp. nov.**

[urn:lsid:zoobank.org:act:AEDDA6F2-E310-4FAA-873D-A001878505A2](http://urn:lsid:zoobank.org:act:AEDDA6F2-E310-4FAA-873D-A001878505A2)

Figs 69–73

**Diagnosis**

Easily distinguished from closest known relatives (*Pa. marilog* Huber sp. nov.; *Pa. dinagat* Huber sp. nov.) by processes arising from near male PME with widened tips (Fig. 71), by morphology of male palp (Figs 69, 70; simple retrolatero-ventral trochanter apophysis; procurus with transparent dorsal flap; appendix with simple tip, short and evenly curved), and by epigynal scape without widening in mid-section (Fig. 72). From other congeners also by male clypeus modification (Fig. 71; patch of ~25 short spines), and by epigynal scape directed toward anterior (Fig. 72).

**Etymology**

The species name is derived from the type locality; noun in apposition.

**Type material**

PHILIPPINES: holotype ♂, in ZFMK (Ar 13013), Luzon, Camarines Sur Province, Mt. Isarog, W slope (13.664°N, 123.34–123.35°E), ~600–900 m a.s.l., forest, on leaves, 23 Feb. 2014 (B.A. Huber).

**Other material examined**

PHILIPPINES: 2 ♀♀ in ZFMK (Ar 13014), same data as holotype.

**Description**

**Male** (holotype)

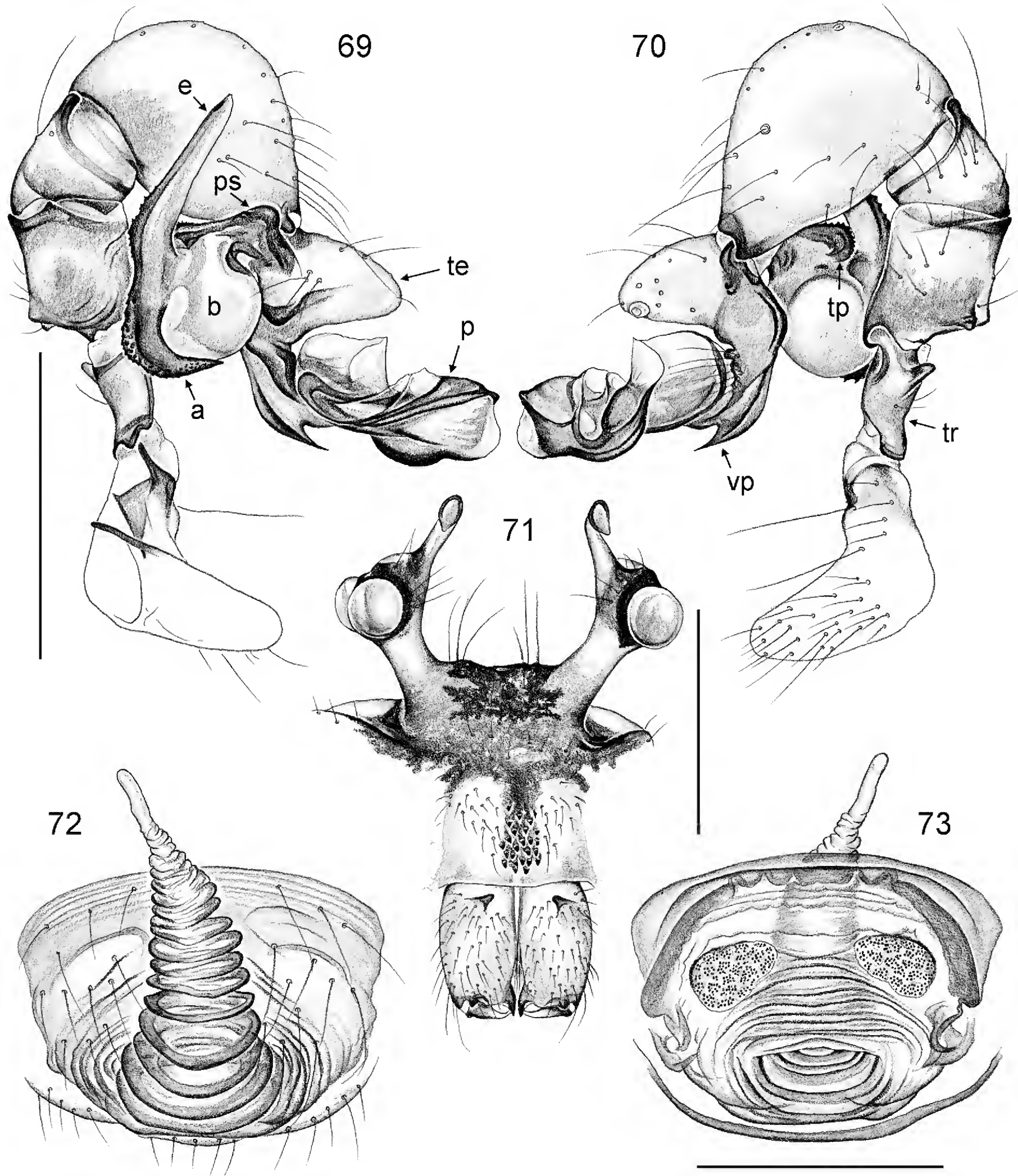
MEASUREMENTS. Total body length 5.2, carapace width 1.1. Leg 1: 38.8 (8.9 + 0.5 + 9.1 + 18.3 + 2.0), tibia 2: 6.1, tibia 3: 3.6, tibia 4: 5.5; tibia 1 L/d: 98. Distance PME–PME 450 µm, diameter PME 90 µm, distance PME–ALE ~40 µm; AME absent.

COLOR. Carapace pale ochre yellow to whitish, without posterior mark, ocular area and clypeus dark brown, with black mark in AME area; sternum whitish; legs ochre-yellow with dark brown patellae and tibia-metatarsus joints; abdomen ochre-gray, with black marks dorsally, monochromous ventrally.

BODY. Habitus similar to *Pa. marilog* Huber sp. nov. and *Pa. dinagat* Huber sp. nov. (cf. Figs 11, 14); ocular area raised, each triad on long stalk, curved process arising from near PME with distinctive widened tip directed toward anterior (Fig. 71); carapace without median furrow; clypeus with distinct field of ~25 short spines, with slightly longer but not stronger hairs below black mark; sternum wider than long (0.70/0.55), unmodified.

CHELICERAE. As in Fig. 71, with pair of simple, weakly sclerotized processes in rather frontal position directed toward median; without modified hairs; without stridulatory ridges.

PALPS. As in Figs 69–70; symmetric; coxa with strong ventro-distal rim but otherwise unmodified; trochanter relatively long, with two simple retrolateral processes; femur short, with two short dorsal processes; tibia short and wide (width ~65% of length); tarsus with short whitish elongation with subterminal tarsal organ; procurus proximal part with pointed ventral process, distal part hinged, very complex, with distinctive dorsal transparent flap; bulb with strong proximal sclerite, with processes extending in opposite directions (dorsal embolus; ventral appendix with many small scales), with small retrolateral toothed process arising from proximal bulbal sclerite, without small round sclerite between appendix and bulb.



**Figs 69–73.** *Panjange isarog* Huber sp. nov. (ZFMK, Ar 13013, 13014). **69–70.** Left male palp, prolateral and retrolateral views. **71.** Male prosoma and chelicerae, frontal view. **72–73.** Cleared female genitalia, ventral and dorsal views. Abbreviations: a = appendix; b = genital bulb; e = embolus; p = procursus; ps = proximal bulbal sclerite; te = tarsal elongation; tp = toothed process of proximal bulbal sclerite; tr = trochanter. Scale bars: 69–71 = 0.5 mm; 72–73 = 0.3 mm.

LEGS. Without spines and curved hairs; few vertical hairs; retrolateral trichobothrium on tibia 1 at 2%; prolateral trichobothrium absent on tibia 1, present on other tibiae; tarsus 1 with > 30 pseudosegments, only distally distinct.

### **Female**

In general similar to male but eye triads on low humps and much closer together (distance PME–PME 250  $\mu$ m); clypeus unmodified. Tibia 1: 6.9, 7.4. Epigynum very small, weakly sclerotized plate with scape directed toward anterior, scape strongly folded, apparently extensible, without widening in mid-section (Fig 72); internal genitalia as in Fig. 73.

### **Distribution**

Known from type locality on Luzon Island only (Fig. 16).

### *Panjange dinagat* Huber sp. nov.

[urn:lsid:zoobank.org:act:A711003E-5B76-4450-B9EE-C618A2200483](http://urn:lsid:zoobank.org:act:A711003E-5B76-4450-B9EE-C618A2200483)

Figs 11–13, 74–78

### **Diagnosis**

Easily distinguished from most known relatives (except *Pa. marilog* Huber sp. nov.) by complex male palpal trochanter apophysis (Fig. 75), and by widening of epigynal scape in mid-section (Fig. 77); from *Pa. marilog* Huber sp. nov. by male pedipalp (Figs 74–75; relatively wider tibia; shorter whitish elongation of tarsus; different shapes of procurus and appendix; more slender embolus) and female genitalia (longer than wide; Fig. 77).

### **Etymology**

The species name is derived from the type locality; noun in apposition.

### **Type material**

PHILIPPINES: holotype ♂, in ZFMK (Ar 13015), Dinagat Island, near Libjo, Paragua Forest, “site 1” (10.222°N, 125.553°E), 130 m a.s.l., forest at brook, on leaves, 20 Feb. 2014 (B.A. Huber, P.N. Banaag).

### **Other material examined**

PHILIPPINES, Dinagat Island: 1 ♂, 3 ♀♀, 2 juvs in ZFMK (Ar 13016), same data as holotype; 1 ♀, 2 juvs in pure ethanol, in ZFMK (Phi 232), same data; 1 ♀ in ZFMK (Ar 13017), near Libjo, Paragua Forest, “site 2” (10.241°N, 125.545°E), 240 m a.s.l., forest along brook, on leaf, 20 Feb. 2014 (B.A. Huber, P.N. Banaag).

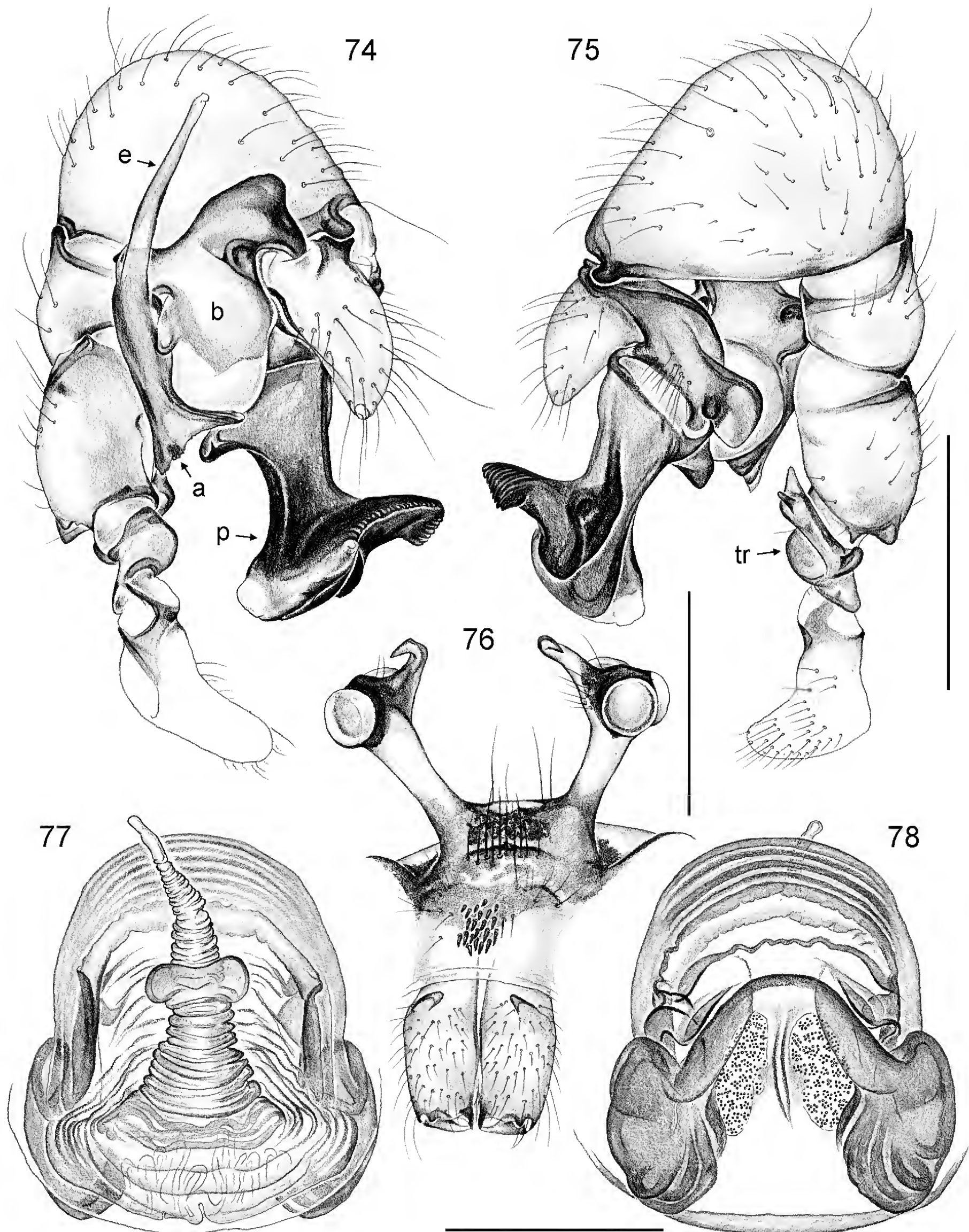
### **Description**

#### **Male (holotype)**

MEASUREMENTS. Total body length 4.4, carapace width 1.0. Leg 1: 33.9 (7.8 + 0.5 + 7.9 + 15.7 + 2.0), tibia 2: 5.0, tibia 3: 2.8, tibia 4: 4.3; tibia 1 L/d: 97. Distance PME–PME 430  $\mu$ m, diameter PME 90  $\mu$ m, distance PME–ALE ~50  $\mu$ m; AME absent.

COLOR. Carapace pale ochre yellow to whitish, without posterior mark, ocular area and clypeus dark brown, with black mark in AME area; sternum whitish; legs ochre-yellow with dark brown patellae and tibia-metatarsus joints; abdomen ochre-gray, with black marks dorsally, monochromous ventrally.

BODY. Habitus as in Fig. 11; ocular area raised, each triad on long stalk, with pointed curved process arising from near PME and directed toward anterior (Fig. 76); carapace without median furrow; clypeus



**Figs 74–78.** *Panjange dinagat* Huber sp. nov. (ZFMK, Ar 13016). 74–75. Left male palp, prolateral and retrolateral views. 76. Male prosoma and chelicerae, frontal view. 77–78. Cleared female genitalia, ventral and dorsal views. Abbreviations: a = appendix; b = genital bulb; e = embolus; p = procurus; tr = trochanter. Scale bars: 74–76 = 0.5 mm; 77–78 = 0.3 mm.

with two patches of modified hairs: slightly stronger hairs below black mark and distinct field of ~20 short spines more distally; sternum wider than long (0.65/0.50), unmodified.

CHELICERAE. As in Fig. 76, with pair of simple, weakly sclerotized processes in rather frontal position directed toward median; without modified hairs; without stridulatory ridges.

PALPS. As in Figs 74–75; symmetric; coxa with strong ventro-distal rim but otherwise unmodified; trochanter relatively long, with simple retrolatero-dorsal process and complex retrolatero-ventral apophysis, distally curved toward prolateral, with two distinctive subdistal branches directed toward distal and retrolateral respectively; femur short, with two short dorsal processes and very indistinct prolateral hump; tibia very thick (width ~70% of length); tarsus with short whitish elongation with terminal tarsal organ; procurus proximal part with rounded ventral process, distal part hinged, with distinctive retrolateral process and simple flat prolateral process; bulb with strong proximal sclerite, long processes extending in opposite directions (dorsal embolus; ventral appendix), with retrolateral toothed process arising from proximal bulbal sclerite, with small round sclerite between appendix and bulb.

LEGS. Without spines and curved hairs; few vertical hairs; retrolateral trichobothrium on tibia 1 at 2%; prolateral trichobothrium absent on tibia 1, present on other tibiae; tarsus 1 pseudosegments barely visible in dissecting microscope.

**Male** (variation)

Tibia 1 in other male: 7.8.

**Female**

In general similar to male but eye triads on low humps and much closer together (distance PME–PME 220 µm); clypeus unmodified. Tibia 1 in 4 females: 5.9, 6.1, 6.1, 6.7. Epigynum weakly sclerotized plate with scape directed toward anterior, scape strongly folded and extensible, with distinctive widening in mid-section (Fig. 77), distal part semitransparent; internal genitalia as in Fig. 78.

**Natural history**

The spiders were found on the undersides of large leaves about 0.5–2 m above the ground.

**Distribution**

Known from type locality on Dinagat Island only (Fig. 16).

*Panjange marilog* Huber sp. nov.

[urn:lsid:zoobank.org:act:0B086DBA-DB8C-4253-AB9C-E932F2697216](https://doi.org/10.21203/rs.3.rs-10000000)

Figs 14–15, 79–89

**Diagnosis**

Easily distinguished from most known relatives (except *Pa. dinagat* Huber sp. nov.) by complex male palpal trochanter apophysis (Fig. 80), and by widening of epigynal scape in mid-section (Fig. 82); from *Pa. dinagat* Huber sp. nov. by male pedipalp (Figs 79–80; relatively more slender tibia; longer whitish elongation of tarsus; different shapes of procurus and appendix; wider embolus) and female genitalia (wider than long; Fig. 82).

**Etymology**

The species name is derived from the type locality; noun in apposition.



### Type material

PHILIPPINES: holotype ♂, in ZFMK (Ar 13018), Mindanao, Davao del Sur Province, Marilog Distr., Baganihan (7.469°N, 125.250°E), 1210 m a.s.l., primary forest near road, on leaves, 15 Feb. 2014 (B.A. Huber, E. Mondejar).

### Other material examined

PHILIPPINES: Davao del Sur Province: 4 ♂♂, 1 ♀ in ZFMK (Ar 13019) and 1 ♂ in MSU-IIT, same data as holotype; 2 ♀♀, 3 juvs in pure ethanol, in ZFMK (Phi 255), same data; 1 ♂, 1 ♀ in ZFMK (Ar 13020), same locality, “site 2” (7.4563°N, 125.2390°E), 6 Dec. 2014 (M.A. Responte); 1 ♂, 2 ♀♀, 3 juvs in ZFMK (Ar 13021) and 1 ♂, 1 ♀ in MSU-IIT, same locality, “site 3” (7.4696°N, 125.2452°E), 7 Dec. 2014 (M.A. Responte). Bukidnon Province: 2 ♂♂, 4 ♀♀, 7 juvs in ZFMK (Ar 13022) and 1 ♂, 1 ♀ in MSU-IIT, all poorly preserved, Imbayao (8.1344°N, 125.0297°E), 9–10 Feb. 2015 (E.P. Mondejar).

### Description

#### Male (holotype)

MEASUREMENTS. Total body length 5.1, carapace width 1.2. Leg 1: 41.2 (9.6 + 0.5 + 9.7 + 19.1 + 2.3), tibia 2: 6.5, tibia 3: 3.8, tibia 4: 5.7; tibia 1 L/d: 97. Distance PME–PME 470 µm, diameter PME 90 µm, distance PME–ALE ~50 µm; AME absent.

COLOR. Carapace pale ochre yellow to whitish, without posterior mark, ocular area and clypeus dark brown, with black mark in AME area; sternum whitish; legs ochre-yellow with dark brown patellae and tibia-metatarsus joints; abdomen ochre-gray, with black marks dorsally, monochromous ventrally.

BODY. Habitus as in Fig. 14; ocular area raised, each triad on long stalk, with pointed curved process arising from near PME and directed toward anterior (Figs 81, 84, 87); carapace without median furrow; clypeus with two patches of modified hairs: slightly stronger hairs below black mark and distinct field of ~20 short spines more distally (Figs 84–85); sternum wider than long (0.70/0.60), unmodified.

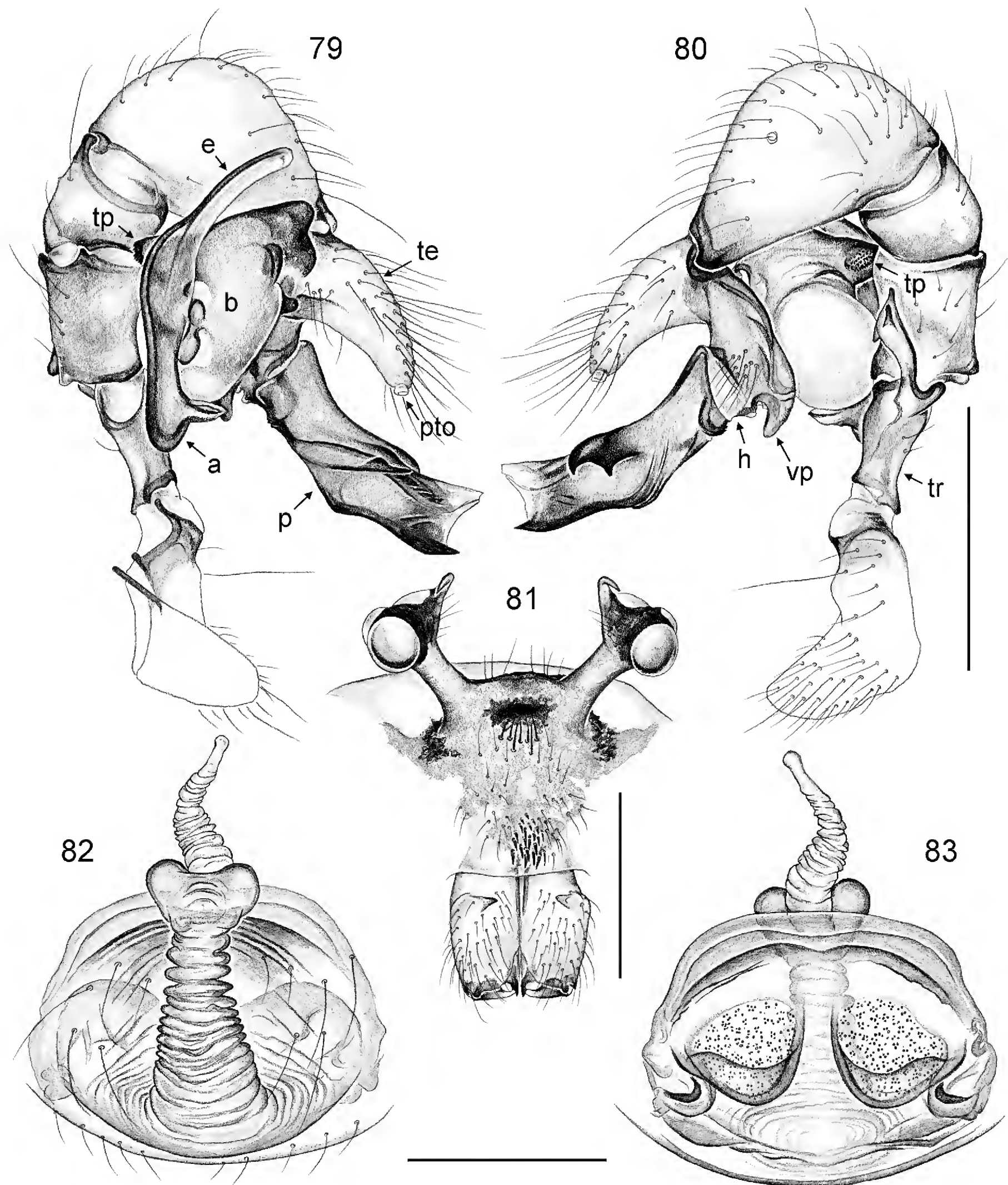
CHELICERAE. As in Figs 81 and 84, with pair of simple, weakly sclerotized processes in rather frontal position directed toward median; without modified hairs; without stridulatory ridges.

PALPS. As in Figs 79–80; symmetric; coxa with strong ventro-distal rim but otherwise unmodified; trochanter relatively long, with simple retrolatero-dorsal process and complex retrolatero-ventral apophysis distally curved toward prolateral, with two distinctive subdistal branches directed toward distal and retrolateral respectively; femur short, with two short dorsal processes and indistinct prolateral hump; tibia very thick (tibia width ~60% of length); tarsus with whitish elongation with terminal capsulate tarsal organ (Fig. 89); procurus proximal part with ventral process, distal part hinged, with distinctive retrolateral process and simple flat prolateral process; bulb with strong proximal sclerite, long processes extending in opposite directions (dorsal embolus; ventral appendix), with retrolateral process arising from proximal bulbal sclerite, with small round sclerite between appendix and bulb.

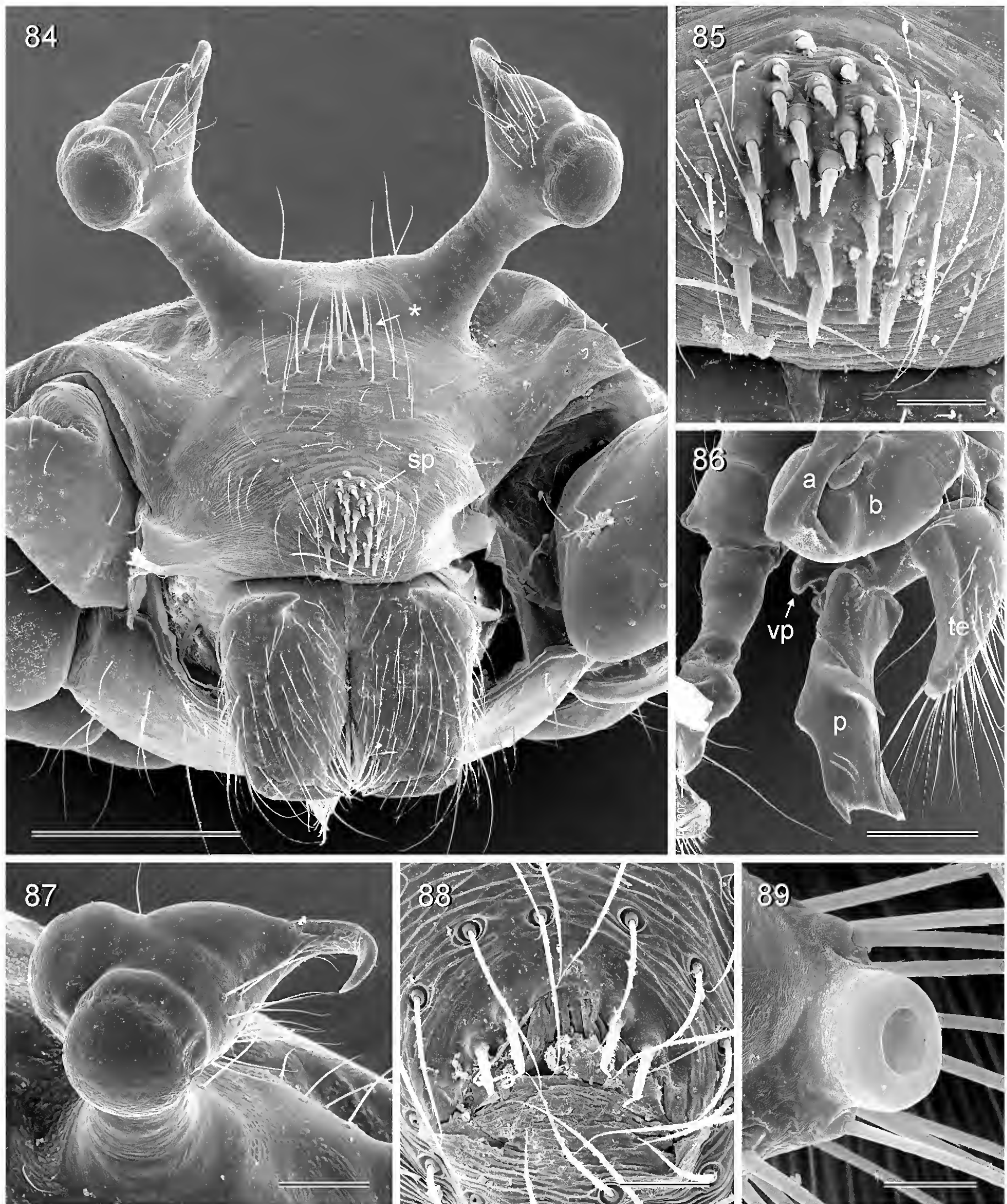
LEGS. Without spines and curved hairs; few vertical hairs; retrolateral trichobothrium on tibia 1 at 2%; prolateral trichobothrium absent on tibia 1, present on other tibiae; tarsus 1 with > 30 pseudosegments, only distally fairly distinct.

#### Male (variation)

Tibia 1 in 10 other males: 9.2–10.4 (mean 9.6). Background color of abdomen with variable shades of reddish to light brown (Figs 14–15).



**Figs 79–83.** *Panjange marilog* Huber sp. nov. (ZFMK, Ar 13019) **79–80.** Left male palp, prolateral and retrolateral views. **81.** Male prosoma and chelicerae, frontal view. **82–83.** Cleared female genitalia, ventral and dorsal views. Abbreviations: a = appendix; b = genital bulb; e = embolus; h = hinge; p = procursus; pto = palpal tarsal organ; te = tarsal elongation; tp = toothed process of proximal bulbal sclerite; tr = trochanter; vp = ventral process. Scale bars: 79–81 = 0.5 mm; 82–83 = 0.3 mm.



**Figs 84–89.** *Panjange marilog* Huber sp. nov., SEM micrographs (ZFMK, Ar 13019). **84.** Male prosoma, frontal view (asterisk marks stronger hairs below ocular area). **85.** Spines on male clypeus. **86.** Left male palp, prolateral view. **87.** Right eye stalk, triad, and hooked process, oblique frontal view. **88.** Male gonopore. **89.** Male palpal tarsal organ. Abbreviations: a = appendix; b = genital bulb; p = procurus; te = tarsal elongation; sp = spines on clypeus; vp = ventral process. Scale bars: 84 = 300  $\mu$ m; 85 = 40  $\mu$ m; 86 = 200  $\mu$ m; 87 = 80  $\mu$ m; 88 = 30  $\mu$ m; 89 = 20  $\mu$ m.

### **Female**

In general similar to male but eye triads on low humps and much closer together (distance PME–PME 240  $\mu\text{m}$ ); clypeus unmodified. Tibia 1 in 4 females: 7.1, 7.3, 7.3, 7.5. Epigynum weakly sclerotized plate with scape directed toward anterior, scape strongly folded, apparently extensible, with distinctive widening in mid-section (Fig. 82), distal part semitransparent; internal genitalia as in Fig. 83.

### **Natural history**

The spiders were found on the undersides of leaves about 0.5–1 m above the ground.

### **Distribution**

Known from two localities on Mindanao Island (Fig. 16).

### *Panjange bukidnon* Huber sp. nov.

[urn:lsid:zoobank.org:act:1B7C5428-F2F6-49B6-BC90-79B2C761F2B7](https://zoobank.org/act:1B7C5428-F2F6-49B6-BC90-79B2C761F2B7)

Figs 90–92

### **Diagnosis**

Easily distinguished from known congeners (and other similar relatives currently in *Pholcus*) by modifications of male ocular area (Fig. 90; short stalks and distinctive processes arising from near PME, with contiguous pointed tips), and by morphology of male palp (Figs 91–92; highly distinctive procurus; shapes of bulbal processes). Female unknown.

### **Etymology**

The species name is derived from the type locality; noun in apposition.

### **Type material**

PHILIPPINES: holotype ♂, in ZFMK (Ar 13023), Mindanao, Bukidnon Province, Santo Domingo (7.782°N, 125.397°E), 560 m a.s.l., forest remnant along brook, on leaf, 8–9 Feb. 2014 (B.A. Huber, E. Mondejar).

### **Other material examined**

None.

### **Description**

#### **Male** (holotype)

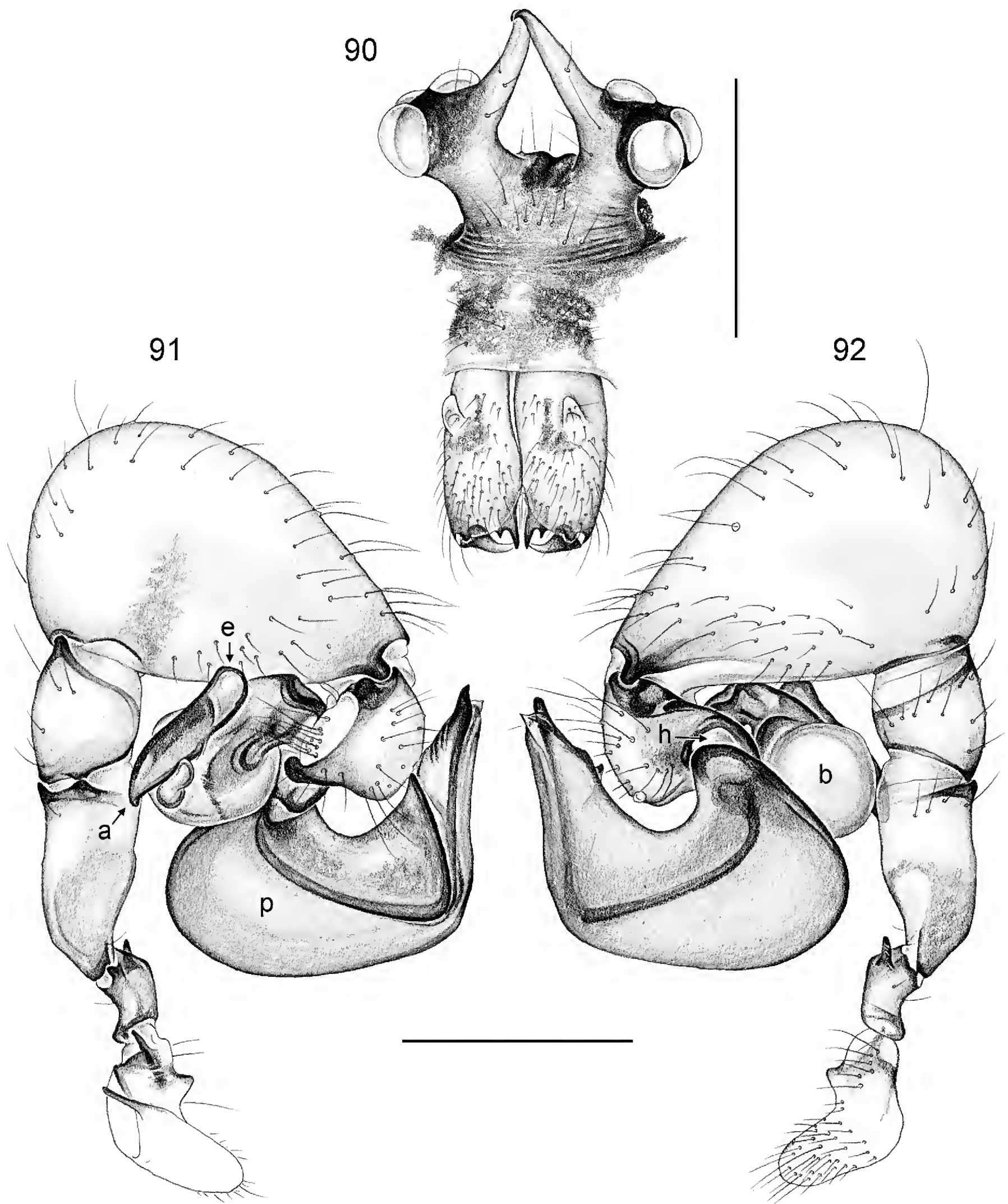
MEASUREMENTS. Total body length 5.0, carapace width 0.9. Leg 1: 9.8 + 0.4 + 9.8, metatarsi broken in both legs, tibia 2: 6.4, tibia 3: 3.7, tibia 4: 5.4; tibia 1 L/d: 110. Distance PME–PME 250  $\mu\text{m}$ , diameter PME 100  $\mu\text{m}$ , distance PME–ALE ~30  $\mu\text{m}$ ; AME absent.

COLOR. Entire spider mostly pale ochre-gray to whitish, except large dark brown mark in ocular area including clypeus, pair of indistinct dark marks posteriorly on carapace, few small dark spots on abdomen dorsally, and brown patellae and tibia-metatarsus joints.

BODY. Habitus similar to *Pa. malagos* Huber sp. nov. (cf. Fig. 5); ocular area raised, each triad on short stalk, with distinctive processes arising from near PME with contiguous tips (Fig. 90); carapace without median furrow; clypeus unmodified; sternum wider than long (0.65/0.55), unmodified.

CHELICERAE. As in Fig. 90, with pair of simple, weakly sclerotized proximal processes in rather frontal position; each lamina with additional small tooth; without modified hairs; without stridulatory ridges.

PALPS. As in Figs 91–92; symmetric; coxa with distinct ventral apophysis; trochanter with short retrolateral apophysis; femur small, barely modified; tibia very large and wide (width ~65% of length); tarsus without elongation; procurus proximal part very short, without ventral process, distal part hinged, very large, without (or with very indistinct) parallel ridges; bulb with strong proximal sclerite, with very



**Figs 90–92.** *Panjange bukidnon* Huber sp. nov. (ZFMK, Ar 13023). **90.** Male prosoma and chelicerae, frontal view. **91–92.** Left male palp, prolateral and retrolateral views. Abbreviations: a = appendix; b = genital bulb; e = embolus; h = hinge; p = procurus. Scale bars = 0.5 mm.

short processes (embolus and appendix) extending in opposite directions, without retrolateral process arising from proximal bulbal process, with small round sclerite between appendix and bulb.

LEGS. Without spines and curved hairs; few vertical hairs; retrolateral trichobothrium on tibia 1 at 4%; prolateral trichobothrium absent on tibia 1, present on other tibiae.

#### **Female**

Unknown.

#### **Distribution**

Known from type locality on Mindanao Island only (Fig. 16).

#### **Discussion**

The *Panjange lanthana* group, previously monotypic (Deeleman-Reinhold & Platnick 1986; Huber 2011), is a diverse group apparently restricted to the Philippines and supported by two synapomorphies. The configuration of the male bulbal sclerites (embolus pointing in opposite direction than appendix) is unique among Pholcidae. A close relationship of the *lanthana* group with the widespread *cavicola* group (Sulawesi to Australia) is strongly supported by the cladistic analysis. However, the relationship of these two groups to the third species group (*nigrifrons* group on Borneo) remains unclear. The characters supporting the monophyly of *Panjange* do not appear particularly convincing: (1) the reduction of the unculus has occurred repeatedly within *Pholcus* (Huber 2011); and (2) the ridges on the procurus are barely visible or absent in some species. In fact, preliminary molecular data (A. Valdez-Mondragón, D. Dimitrov, B.A. Huber unpublished data) suggest *Panjange* might not be monophyletic.

Spider genital asymmetry is apparently exceedingly rare, and to our knowledge has been documented in only nine of currently 3959 extant spider genera (genus count from World Spider Catalog 2015). Most cases are in Pholcidae (independent origins in *Mesabolivar* González-Sponga, 1998, *Metagonia* Simon, 1893, and *Panjange*; Huber 1997b, 2004, 2006; herein), and Oonopidae (presumably independent origins in *Lionneta* Benoit, 1979, *Escaphiella* Platnick & Dupérré, 2009, *Aschnaonops* Makhan & Ezzatpanah, 2011, and *Paradysderina* Platnick & Dupérré, 2011; Burger 2010; Platnick & Dupérré 2009, 2011; Platnick *et al.* 2013). Further cases have been reported in Theridiidae (*Asygyna* Agnarsson, 2006; Agnarsson 2006) and Oxyopidae (*Oxyopes* Latreille, 1804; Brady 1964, 1975). An attempt to explain the rarity of this phenomenon in spiders (as opposed to the ubiquity in insects) was made in Huber *et al.* (2007). This explanation centers on the fact that one-sided mating positions are an option for neopteran insects with their unpaired intromittent organ but not for spiders with their paired palps. While this may explain the rarity in spiders, it does not explain those few cases where asymmetry did evolve. A previous idea, that spider asymmetry may usually originate in the female as a result of space constraints (Huber 2004, 2006; Huber *et al.* 2007) may apply to certain taxa (e.g., *Asygyna*, *Mesabolivar*, *Metagonia*) but apparently not to others. In Oonopidae, most cases of asymmetry seem to be restricted to males. However, routine preparations of female internal genitalia may simply fail to reveal subtle asymmetries. In fact, the only oonopid case of female asymmetry was discovered by serial sectioning and SEM of internal structures (Burger 2010). The same may apply to the three *Panjange* spiders with male asymmetric genitalia described herein. In two of them (*Pa. malagos* Huber sp. nov.; *Pa. camiguin* Huber sp. nov.), the female genitalia appear symmetric; in the third (*Pa. casaroro* Huber sp. nov.), it is not clear if the apparent asymmetry is an artifact of preparation or not. Further anatomical study with adequate sample sizes is needed to evaluate female symmetry vs. asymmetry in these species.

Sexually dimorphic eye-stalks have been studied in much detail in stalk-eyed flies (e.g., Burkhardt & de la Motte 1988; Wilkinson & Dodson 1997; Panhuis & Wilkinson 1999; Baker & Wilkinson 2001). For these insects, the general consensus is that sexual selection in the context of a resource-defense

mating system has been the driving force in the repeated evolution of exaggerated male eye stalks, both by male-male competition and by female choice. In linyphiid spiders, modifications of the male “head” are apparently always accompanied by glands that discharge their products through pores easily visible in the SEM (Schaible *et al.* 1986). Sexual selection by female choice (via gustatorial courtship) is the most plausible explanation for this group of spiders (Vanacker *et al.* 2003; Kunz *et al.* 2012), but the few species with real eye stalks (such as *Walckenaeria acuminata* Blackwall, 1833) have never been studied in detail. The same is unfortunately true of certain theridiid spiders with similar long eye stalks [e.g., *Phoroncidia longiceps* (Keyserling, 1886); see Levi 1964]. In Pholcidae, nothing is known about the use of the highly sexually dimorphic eye stalks. Glands and pores have been found in the male eye turrets of *Modisimus culicinus* (Simon, 1893) (Huber 1997a) but in none of the *Panjange* spiders studied herein and in none of the stalk-eyed *Pholcus* studied previously with the SEM (Huber 2011). Neither fights nor matings have ever been observed in any *Panjange* species or in any stalk-eyed *Pholcus*. The facts that these spiders were hard to find at all localities and that the low abundance seemed to result from the rarity of suitable large leaves suggest that a resource-defense mating system like in stalk-eyed flies is a plausible working hypothesis for future studies.

Elongated genital structures in spiders are widespread, but it is usually the male intromittent structures and the corresponding female internal ducts that become long and exaggerated. In most cases, this concerns the sperm transfer organ (the embolus) and the corresponding insemination ducts (reviewed in Eberhard & Huber 2010). However, other intromittent structures may go through analogous developments, as for example male procurus and female uterus externus folds in *Mesabolivar yuruani* (Huber, 2000) (see Huber 2006; under *Kaliana yuruani*); or male tibia apophysis and a novel female tubular system in *Hortipes gigapophysalis* Jocqué, Bosselaers & Henrard, 2012 (Jocqué *et al.* 2012). In Filistatidae, it is the basal palpal segments rather than the intromittent embolus that may become elongated (Marusik & Zamani 2015). In this group, cannibalism might appear a plausible explanation because the long palp allows the male body to remain out of reach for the female jaws (e.g., Gerhardt 1928, fig. 2). However, observations have suggested female cooperation rather than aggression (Gerhardt 1928, 1930). In *Panjange* spiders, elongation likewise involves male structures that are very likely not inserted into the female. Instead, the palpal elongation in this group appears related to the extensible scape in the female. Both in *Calapnita* and in *Panjange*, the species with the longest male palps also have the longest female scapes (*Calapnita semengoh* Huber, 2011; *Pa. hamiguitan* Huber sp. nov.). This suggests that males and females may be engaged in an arms race (cf. Kuntner *et al.* 2009), with ever longer scapes requiring ever longer palps. The fact that pholcid chelicerae contact the female during copulation in all cases studied (reviewed in Huber 1999) suggests that palpal elongation is not related to cannibalism avoidance by keeping the body far from the female. In sum, a wide variety of factors may lead to genital elongation in spiders, but direct functional observations are almost entirely missing.

## Acknowledgements

We thank our driver Vicente Bulongon for bringing us safely to all requested places; the students Mae A. Responte, Maria B.R. Dacar, Eddie P. Mondejar and Philip N.O. Banaag II for help in the field and for contributing specimens from their own research; Matjaz Kuntner and an anonymous reviewer for comments that helped improve the manuscript; the Department of Environment and Natural Resources (DENR) CARAGA, DENR Region X, and DENR Region XI for issuing the relevant permits; and the German Research Foundation for financial support (DFG Project HU 980/11-1).

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**Appendix 1.** Data matrix for cladistic analysis. Taxa are arranged as in the cladogram in Fig. 1. Terminals and characters are detailed in Appendices 2 and 3. - = non-applicable; ? = unknown or coding ambiguous. This matrix is available online at [www.pholcidae.de/matrices.html](http://www.pholcidae.de/matrices.html)

	<b>5</b>	<b>10</b>	<b>15</b>	<b>20</b>	<b>25</b>	
	↓	↓	↓	↓	↓	
<i>Quamtana</i> sp.	01	--	0000000	-000	-0001000	--0
<i>Pholcus phalangioides</i>	01	--	0000000	-000	-0000000	--0
<i>Pholcus debilis</i>	01	--	0000000	-000	-0000000	--0
<i>Pholcus phui</i>	01	--	001-001	00000	-0001000	--0
<i>Pholcus diopsis</i>	00	000000	1000	-000	-0000000	--0
<i>Pholcus atrigularis</i>	00	000000	1000	-000	-0000000	--0
<i>Pholcus minang</i>	00	000000	1000	-000	-0000000	--0
<i>Pa. Bor 96</i>	00	000000	1001	0000	100001000	--0
<i>Pa. Bor 11</i>	00	000000	1001	1001	00001000	--0
<i>Pa. bako</i>	00	000000	1001	1001	00001000	--1
<i>Pa. Bor 78</i>	00	000000	1001	1001	00001000	--1
<i>Pa. sedgwicki</i>	00	000000	1001	1001	0001100	????
<i>Pa. iban</i>	01	--	000100	1100	100011000	--1
<i>Pa. nigrifrons</i>	01	--	000100	1100	10011000	--1
<i>Pa. Bor 100</i>	01	--	000100	1100	100111000	--1
<i>Pa. Bor 109</i>	01	--	000100	1100	100111000	--1
<i>Pa. cavicola</i>	00	10001	-000	-01	??001?0100?	
<i>Pa. alba</i>	00	10001	-000	-111	10001001000	
<i>Pa. mirabilis</i>	00	10001	-000	-111	10001001000	
<i>Pa. madang</i>	00	10001	-000	-111	10001001000	
<i>Pa. dubia</i>	00	10001	-000	-111	10001001000	
<i>Pa. lanthana</i>	01	--	001-000	-011	01001011000	
<i>Pa. malagos</i> Huber sp. nov.	00	10001	-100	-011	01001011001	
<i>Pa. casaroro</i> Huber sp. nov.	10	11001	-100	-011	01001011000	
<i>Pa. camiguin</i> Huber sp. nov.	10	11001	-100	-011	01001011000	
<i>Pa. hamiguitan</i> Huber sp. nov.	00	00000	1-000	-110	01001011000	
<i>Pa. isarog</i> Huber sp. nov.	00	10011	-000	-000	-1001111100	
<i>Pa. dinagat</i> Huber sp. nov.	00	10111	-010	-000	-1001111110	
<i>Pa. marilog</i> Huber sp. nov.	00	10111	-010	-000	-1001111110	

**Appendix 2.** Terminal taxa scored for the cladistic analysis, with origin and depository. Taxa are arranged as in the cladogram in Fig. 1. Collection codes used in this appendix only: AMNH = American Museum of Natural History, New York; IRSB = Institut Royal des Sciences Naturelles de Belgique, Brussels; MZPW = Museum of the Institute of Zoology, Polish Academy of Science, Warsaw; QMB = Queensland Museum, Brisbane; RMNH = Netherlands Centre for Biodiversity Naturalis, Leiden.

### Outgroups

*Quamtana* sp.: for the present matrix, all known species of *Quamtana* Huber, 2003 share the same coding. For this reason, no particular species is specified.

*Pholcus phalangioides* (Fuesslin, 1775): Germany, Bonn (ZFMK)

*Pholcus debilis* (Thorell, 1899): Cameroon, Mt. Koupe (ZFMK)

*Pholcus phui* Huber, 2011: Thailand, Hala Bala WS (ZFMK)

*Pholcus diopsis* Simon, 1901: Thailand, Wat Kuhapimuk (ZFMK)

*Pholcus atrigularis* (Simon, 1901): Malaysia, Ulu Dong (ZFMK)

*Pholcus minang* Huber, 2011: Indonesia, Sumatra, Kerinci N.P. (RMNH)

### Panjange

*Pa.* Bor 96: Malaysia, Sarawak, Pueh (ZFMK)

*Pa.* Bor 11: Malaysia, Sarawak, Niah (ZFMK)

*Pa. bako* Huber, 2011: Malaysia, Sarawak, Bako (RMNH)

*Pa.* Bor 78: Malaysia, Sarawak, Kapit (ZFMK)

*Pa. sedgwicki* Deeleman-Reinhold & Platnick, 1986: Malaysia, Sarawak, nr Kapit (AMNH)

*Pa. iban* Huber, 2011: Malaysia, Sarawak, Semengoh (ZFMK)

*Pa. nigrifrons* Deeleman-Reinhold & Deeleman, 1983: Indonesia, Kalimantan, Sepaku (RMNH)

*Pa.* Bor 100: Malaysia, Sarawak, Penrissen (ZFMK)

*Pa.* Bor 109: Malaysia, Sarawak, Kubah (ZFMK)

*Pa. cavicola* Deeleman-Reinhold & Deeleman, 1983: Indonesia, Sulawesi, nr Camba (RMNH)

*Pa. alba* Deeleman-Reinhold & Deeleman, 1983: Indonesia, Sulawesi (RMNH)

*Pa. mirabilis* Deeleman-Reinhold, 1986: Australia, Queensland, Gordon Creek (QMB)

*Pa. madang* Huber, 2011: Papua New Guinea, Baiteta (IRSB)

*Pa. dubia* (Kulczyński, 1911): Indonesia, New Guinea (RMNH, MZPW)

*Pa. lanthana* Deeleman-Reinhold & Deeleman, 1983: Philippines, Luzon, Mt. Isarog (ZFMK)

*Pa. malagos* Huber sp. nov.: Philippines, Mindanao, Malagos (ZFMK)

*Pa. casaroro* Huber sp. nov.: Philippines, Negros, Casaroro Falls (ZFMK)

*Pa. camiguin* Huber sp. nov.: Philippines, Camiguin, Katibawasan Falls (ZFMK)

*Pa. hamiguitan* Huber sp. nov.: Philippines, Mindanao, Mt. Hamiguitan (ZFMK)

*Pa. isarog* Huber sp. nov.: Philippines, Luzon, Mt. Isarog (ZFMK)

*Pa. dinagat* Huber sp. nov.: Philippines, Dinagat, Paragua (ZFMK)

*Pa. marilog* Huber sp. nov.: Philippines, Mindanao, Baganihan (ZFMK)

**Appendix 3.** Characters scored for cladistic analysis.

**Male prosoma**

1. Eye stalks: (0) short, i.e. up to  $3 \times$  as long as wide; (1) long, i.e. more than  $6 \times$  as long as wide. Extremely long eye stalks are shared by *Pa. casaroro* Huber sp. nov. and *Pa. camiguin* Huber sp. nov. (Figs 28, 35).
2. Pointed processes arising from near PME: (0) present (e.g., Figs 17, 28, 66); (1) absent. Such processes occur in *Panjange* and in several species currently included in *Pholcus* (Huber 2011). They are thus considered plesiomorphic for *Panjange*, where they have been secondarily lost in *Pa. lanthana* and within the *nigrifrons* group.
3. Ocular pointed processes, shape: (0) straight or slightly curved (Fig. 66); (1) strongly curved or hooked (Figs 48, 87). Strongly curved ocular processes unite the *Panjange cavicola* and *lanthana* groups. In *Pa. hamiguitan* Huber sp. nov. the processes are considered secondarily straight.
4. Ocular pointed processes, tips: (0) not contacting each other; (1) contacting and parallel to each other. The unique configuration of the two processes forming an apparent functional unit (the dorsal one lying in a groove of the ventral one) is shared by *Pa. casaroro* Huber sp. nov. and *Pa. camiguin* Huber sp. nov. (Figs 48, 49). The processes are similar in *Pa. bukidnon* Huber sp. nov. (Fig. 90) but there the tips lie simply side by side.
5. Ocular area, strong hairs on frontal side: (0) absent; (1) present. Strong hairs (Fig. 84; in addition to spines more distally on the clypeus, see character 6) are shared by *Pa. dinagat* Huber sp. nov. and *Pa. marilog* Huber sp. nov.
6. Clypeus spines: (0) absent; (1) present. The presence of such spines (Figs 84, 85) is a synapomorphy of *Pa. isarog* Huber sp. nov., *Pa. dinagat* Huber sp. nov., and *Pa. marilog* Huber sp. nov.
7. Distal cheliceral apophyses: (0) present; (1) absent. The absence of distal cheliceral apophyses unites the *Panjange cavicola* and *lanthana* groups.
8. Distal cheliceral apophyses, shape: (0) simple; (1) bipartite. A bipartite apophysis characterizes the *Panjange nigrifrons* group as well as several outgroup species (*Pholcus diopsis*; *Pholcus atrigularis*; *Pholcus minang*) (e.g., figs 476, 640, 664, 690 in Huber 2011). It is thus considered plesiomorphic for *Panjange*.

**Male palps**

9. Pedipalp asymmetry: (0) absent; (1) present. Asymmetry is here interpreted as having evolved once, uniting three species in the southern Philippines (*Pa. malagos* Huber sp. nov., *Pa. casaroro* Huber sp. nov., and *Pa. camiguin* Huber sp. nov.).
10. Trochanter, retrolatero-ventral apophysis: (0) absent or with simple tip; (1) with complex bifid tip and subdistal prolateral side-branch (Figs 75, 80). A complex retrolatero-ventral apophysis unites *Pa. dinagat* Huber sp. nov. and *Pa. marilog* Huber sp. nov.
11. Femur ventral apophysis: (0) absent; (1) present. A distinct ventral process (rather than just a bulging area) characterizes the *Panjange nigrifrons* group (e.g., figs 470, 490 in Huber 2011) and is here interpreted to have evolved independently in *Pholcus phui*.
12. Femur ventral apophysis, shape: (0) about as long as wide and not directed toward distal; (1) longer than wide and directed toward distal (e.g., figs 470, 490 in Huber 2011). A relatively long apophysis unites most species of the *Panjange nigrifrons* group.
13. Tibia shape: (0) not elongated, i.e. less than  $3 \times$  as long as wide; (1) elongated, i.e. more than  $3 \times$  as long as wide. An elongated tibia characterizes most species of the *Panjange cavicola* group (except *Pa. cavicola* itself) and has independently evolved in a much more extreme way in *Pa. hamiguitan* (Figs 64, 65).
14. Tarsal elongation: (0) absent or short (less than  $1.5 \times$  as long as wide at basis) (Figs 70, 75, 80); (1) long (longer than  $2 \times$  as long as wide) (e.g., Figs 19, 39, 65). A strong elongation of the tarsus unites the *Panjange cavicola* and *lanthana* groups, but a reversal occurs within the *lanthana* group, uniting *Pa. isarog* Huber sp. nov., *Pa. dinagat* Huber sp. nov., and *Pa. marilog* Huber sp. nov.

15. Procursus ridges: (0) absent; (1) present (e.g., Figs 18, 26, 52). A series or parallel ridges on the procurus has been proposed as a synapomorphy of *Panjange* before (Huber 2011). In some of the newly described species, these ridges are (apparently secondarily) either indistinct or even absent (*Pa. hamiguitan* Huber sp. nov., *Pa. isarog* Huber sp. nov., *Pa. dinagat* Huber sp. nov., and *Pa. marilog* Huber sp. nov.).
16. Procursus ridges, number: (0) many; (1) only 2–3. Many ridges occur in most species of the *Panjange nigrifrons* group (e.g., figs 470, 490 in Huber 2011) except in *Pa. nigrifrons* itself and in several species of the *lanthana* group (e.g., Figs 18, 26, 52). This condition is thus interpreted to be plesiomorphic for *Panjange*. Other than in *Pa. nigrifrons*, a reduction has occurred in the *cavicola* group (the condition in *Pa. cavicola* is not clear).
17. Procursus ventral process: (0) absent; (1) present. This process seems to unite the *Panjange lanthana* group. It is very distinct in some species (*Pa. lanthana*, see fig. 437 in Huber 2011; *Pa. casaroro* Huber sp. nov., Fig. 27; *Pa. hamiguitan* Huber sp. nov., Fig. 65; *Pa. isarog* Huber sp. nov., Fig. 70; *Pa. dinagat* Huber sp. nov., Fig. 75; *Pa. marilog* Huber sp. nov., Fig. 80), but indistinct in others (*Pa. malagos* Huber sp. nov., Fig. 19; *Pa. camiguin* Huber sp. nov., Fig. 42).
18. Procursus retrolateral transversal sclerite: (0) absent; (1) present. A distinctive transversal sclerite characterizes two undescribed species closely related to *Panjange nigrifrons*.
19. Procursus tip, shape: (0) not flat and widened; (1) flat and widened. A flat and widened procurus tip (e.g., fig. 470 in Huber 2011; fig. 3 in Deeleman-Reinhold & Platnick 1986) unites several species of the *Panjange nigrifrons* group.
20. Uncus on genital bulb: (0) absent; (1) present. Most *Pholcus* species have a distinct bulbal sclerite in addition to the appendix, the so-called uncus. Since *Panjange* seems to be nested within a currently paraphyletic *Pholcus* (Huber 2011), the absence of an uncus in *Panjange* is here considered to be secondary. This reduction has been suggested as a potential synapomorphy of *Panjange* before (Huber 2011), but *Pholcus phui* (and other species not included in the matrix) share this absence and may be closer to *Panjange* than suggested by the cladogram in Fig. 1.
21. Toothed sclerotized process of proximal bulbal sclerite: (0) absent; (1) present. This sclerite (Figs 69, 74, 79) unites three species in the *Panjange lanthana* group (*Pa. isarog* Huber sp. nov., *Pa. dinagat* Huber sp. nov., and *Pa. marilog* Huber sp. nov.). It reminds of an uncus but is here considered a novel structure because it is situated behind the embolus (in prolateral view), while the uncus is situated in front of the embolus.
22. Embolus, direction: (0) parallel to appendix; (1) in opposite direction than appendix. An embolus that points in the opposite direction than the appendix (e.g., Figs 18, 64, 69) is a highly unusual character and is here considered a (strong) synapomorphy of the *Panjange lanthana* group.

### Female genitalia

23. Scape: (0) absent or short, not strongly folded; (1) present, strongly folded and extensible. A strongly folded and extensible scape (e.g., Figs 22, 67, 72) unites the *Panjange cavicola* and *lanthana* groups.
24. Scape, direction: (0) toward posterior; (1) toward anterior. Three species of the *Panjange lanthana* group (*Pa. isarog* Huber sp. nov., *Pa. dinagat* Huber sp. nov., *Pa. marilog* Huber sp. nov.) are united by a scape that is directed toward anterior (Figs 72, 77, 82).
25. Scape, widening: (0) absent; (1) present. Two species of the *Panjange lanthana* group (*Pa. dinagat* Huber sp. nov., *Pa. marilog* Huber sp. nov.) are united by a scape that has a distinctive widened area at about half its length (Figs 77, 82).
26. Female internal genital folds: (0) absent or weakly developed; (1) strongly developed. Most species of the *Panjange nigrifrons* group share a system of strongly developed folds of unknown significance in the female internal genitalia (e.g., figs 473 and 492 in Huber 2011).